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PHYSIOLOGICAL AND BIOCHEMICAL STUDIES IN PLANT METABOLISM

IV. EFFECT OF ILLUMINATION AND DARKNESS ON THE PHYSIOLOGICAL HETEROGENEITY IN THE FIRST LEAF OF WHEAT[1]

BY D. W. A. ROBERTS[2]

Abstract

The respiratory rate, soluble nitrogen content, protein nitrogen content, water content, reducing substance content, and sucrose content of each of the four quarters of the first leaf of Khapli wheat have been determined after different exposures to light under standardized conditions. The respiratory rate of the different quarters and of the leaf as a whole is not determined by the distribution of any of the above mentioned constituents. Protein, water, and sucrose distribution appear to be correlated with the anatomy of the leaf. Leaf anatomy is apparently an important consideration in the physiological heterogeneity of the first leaf of wheat.

Introduction

During their growth the wheat plants grown under the standard conditions used for their culture in this laboratory were subjected to alternating periods of illumination and darkness. In the case of most plants this causes an accumulation of starch and sucrose in the leaves in the daytime, together with an increased respiration rate. On account of the fact that sugar can be removed from the leaf only through the basal part, it is natural to expect that, if sugar concentration is an important factor in controlling the respiratory rate, there should be increased sugar concentration and respiration in the tip of the leaves in the daytime, and low sugar content and respiration rates there after a prolonged period of darkness. It was therefore hoped that the respiratory gradient which has been previously reported to occur in the leaves of wheat (2) would be found to vary diurnally or under the influence of prolonged periods of light and darkness. It was with a view to producing this type of change in the respiratory gradient of wheat leaves that the following series of experiments were undertaken, in an attempt to elucidate the factors responsible for the existence of a gradient in the leaves of Khapli Emmer wheat (*Triticum dicoccum* Schubler. var. Khapli).

[1] *Manuscript received June 14, 1951.*

A contribution from the Department of Botany, University of Toronto. An abridgement of part of a thesis presented in 1948 to the University of Toronto in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

[2] *Plant Physiologist, Dominion Laboratory of Botany and Plant Pathology, Lethbridge, Alta.*

[The August number of this Journal (Can. J. Botany, 29 : 299-449. 1951) was issued August 16, 1951.]

In an earlier publication (9), to which reference should be made, the respiration record of starving isolated wheat leaves has been described (cf. Fig. 3) and the effect of stimulation resulting from the handling of the leaves during isolation has been discussed. Consequently these points, though pertinent, will not be considered here.

Methods

The plants of Khapli Emmer wheat were grown under controlled artificial conditions as described earlier (2, 9). They were subjected to a 12 hr. day of 500 ft-c. intensity produced by eight 500 w. tungsten filament incandescent lights.

In the present set of experiments only the first leaf from plants 13 days old was used. These leaves were cut at the ligule, placed in distilled water in diffuse light, individually quartered, the quarters stored in a moist chamber temporarily, and then weighed before being placed in a respiration chamber. The oxygen uptake of the leaf samples was then determined by the Barcroft manometers as described by Dixon (1). Samples for the determination of oxygen uptake were taken on the 13th day after different periods of illumination and darkness on the day of harvest.

Before a comparison of the respiration rates of the quarters can be made, a suitable measure of the rate of oxygen uptake must be chosen. The half hour readings from the Barcroft manometers vary too much among themselves to be a suitable measure of the respiration rate. In the Pettenkofer experiments, the value obtained for the first three hour period may be used as a measure of the respiration rate of the leaves. This datum can easily be calculated for the Barcroft records. This value, however, suffers from the serious disadvantage that its magnitude is greatly influenced by stimulatory phenomena (9) which can not be avoided. It will not be used in the present analysis since it is possible to use the measure of respiration rate to be called the stabilized respiration rate. The average respiration rate for the first three hours of the starvation air line will be called the "three hour respiration rate".

The "stabilized respiration rate" is the average value of the level phase (9) of the Barcroft starvation air lines. Unfortunately, as was pointed out in the preceding paper of this series (9), the value obtained in this way is also influenced by stimulatory phenomena. However, it is felt that the effect of stimulation on this datum is less than it is on the "three hour respiration rate". An extreme example of this was given in the preceding paper where it was reported in the case of the Pettenkofer records of the quarters, that the "three hour respiration rate" for the whole leaves as calculated from the sum of the rates for the individual quarters was 48 mgm. of carbon dioxide per 100 gm. fresh weight per hour as against approximately 40 mgm. carbon dioxide per 100 gm. fresh weight per hour for whole leaves not quartered, while if the "stabilized rates" for these experiments were considered the discrepancy was much less.

In the determinations of the constituents of the wheat leaves the 13-day-old leaves were roughly quartered instead of being exactly quartered as in the case of the respiration experiments.

All other details of culture were the same as in the respiration experiments. The nitrogenous constituents were divided into soluble nitrogenous substances and coagulable and indiffusible (hereafter referred to as protein) nitrogenous substances. The methods used for these determinations have been described earlier (8). The reducing substances (for the most part probably not sugars) and sucrose were also determined as described in earlier publications (3, 7, 10). The water content determinations were made by drying the leaf samples for not less than two days at room temperature over calcium chloride in a desiccator. In the case of respiration samples, the water content determinations were made on the same samples as the respiration measurements. In the biochemical experiments parallel samples, harvested at the same time, were used for water content determinations.

Changes in the Respiration Rate Induced by Light and Dark

The experimental data on the effect of illumination and darkness on the respiration rate of the quarters of wheat leaves are presented in Fig. 1. The points shown are the average values of three separate determinations made on sets of plants grown separately.

Fig. 1 shows that there is a regular diurnal rise in the rate of oxygen uptake during the period of illumination, and a fall in the rate during the dark period in all four quarters. These results are similar to the results of Krotkov (4) who worked with the whole leaves from greenhouse grown plants. In the case of the fourth quarter, there is a slight rise in the respiratory rate between 8 and 12 hr. of darkness. This is probably associated with the peculiarity in the respiration record of starving basal quarters, subsequently described and named the "darkness hump". This same phenomenon is reflected in the third quarters, where there is only a small drop in the respiratory rate between Hour 8 and Hour 12 of the dark phase. It is peculiar, and at present inexplicable, that the respiratory rate of the fourth quarter should fall during the early phases of the period of illumination.

If the period of darkness is prolonged beyond 12 hr., the different quarters behave quite differently. The two upper quarters undergo a rapid increase in the rate of oxygen uptake, which appears to be followed by a decline in rate after about the 20th hour of darkness. In the two basal quarters, the respiration rate falls still further if the period of darkness is prolonged beyond 12 hr., but this falling rate is finally replaced by a rising rate. If the period of illumination is prolonged beyond 12 hr., the rate of oxygen uptake increases steadily in most cases, when this rate is calculated on the basis of fresh weight. In the tip two quarters, there is indication of a check in this rising rate soon

after the 16th hour of illumination. When the rates are calculated on the basis of dry weight, there is little or no increase in the rate of respiration between the 16th and 28th hour of continuous illumination in the upper two

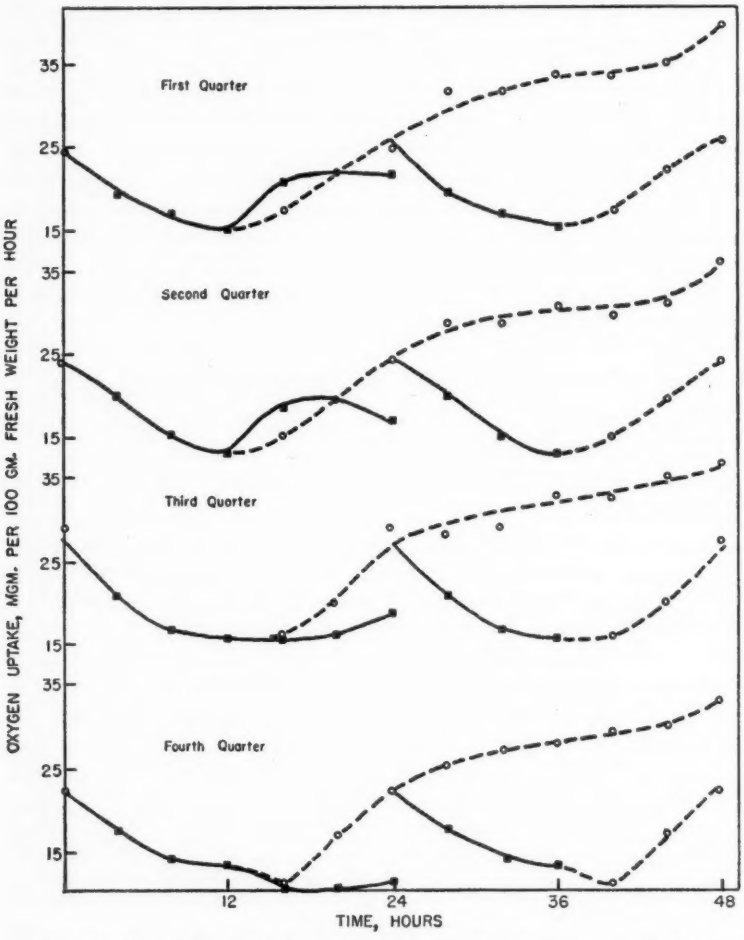

FIG. 1. Diurnal changes in the respiration rates of the four quarters of wheat leaves. The solid lines represent the periods of darkness, the broken lines the periods of illumination. The zero hour represents the close of the period of illumination at the end of the 12th day after planting. The graphs also show the course of the respiration rate if the period of darkness or illumination is continued beyond the normal period of 12 hr.

quarters. In the two lower quarters there is a slow steady increase in the rate of oxygen uptake, when calculated on the dry weight basis from the 16th to the 36th hour of illumination, and probably longer. In almost all

other respects the plot of the dry weight respiration rates during varying experiences of light and darkness, is similar to the stabilized fresh weight values plotted in Fig. 1. The "three hour fresh weight respiration rate" values also give a similar picture. In case of both these other types of value, the third quarter rate after 12 hr. of darkness is greater than the rate after eight hours of dark or four hours of illumination. This is probably associated with the "darkness hump" which is largely confined to the third and fourth quarters.

Changes in the Respiratory Gradient Induced by Light and Darkness

In Fig. 2 the data which have just been discussed are presented in such a way that the changes in the respiratory gradient induced by varying exposures to light and darkness can be examined. Most of the gradients in fresh weight respiration rate are similar to the arbitrarily chosen standard gradient which is the one shown after 12 hr. of illumination. With prolonged exposure to light there is a tendency for the difference in respiration rate between the tip and basal quarters to increase. It is of importance to note that the respiratory gradient does not increase markedly during the early part of the period of illumination. In the case of leaves darkened continuously for 16 hr., a strong gradient is developed with maximum rates of respiration in the tip of the leaves, and minimum rates in the basal quarter. In addition to this major change in the gradient which occurs after prolonged darkness, there appear to be other minor changes in the respiratory gradient, especially during periods of prolonged light. It is possible that changes in gradient that occur after 12 hr. of darkness are comparable with those caused by the transpositional hump in starving isolated leaves. However, except for the timing of events, there is no evidence to prove that the increase in the respiratory rate occurring in the two upper quarters after 12 hr. of darkness is due to the same factors that cause the appearance of the transpositional hump in these same two quarters. In all cases it will be seen that the respiration rate of the basal quarter is the lowest. This has always been found to be the case in mature leaves except those from plants grown under conditions of severe drought.

In Fig. 2 the gradients in the rate of oxygen uptake calculated on the basis of dry weight are also given. Omitting the gradients of leaves having more than 12 hr. of continuous darkness, most of the leaves show that the greatest rate of oxygen uptake occurs in the third quarter, with decidedly lower values in the tip quarter and frequently also in the basal quarter. After 16 to 20 hr. of darkness, the gradient is, however, quite different with high respiration rates in the two upper quarters, and low rates in the two basal quarters. Beside this major modification in the respiratory gradient, there seem to be many smaller changes brought about by differences in exposure to light and darkness.

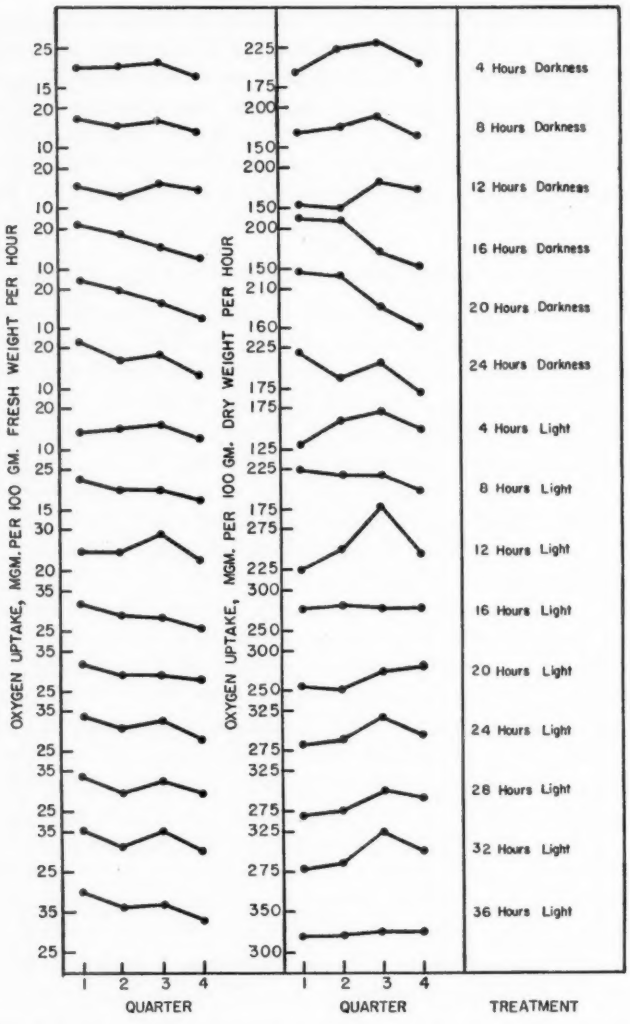

FIG. 2. The respiration gradients in wheat leaves harvested after various periods of illumination or darkness.

Changes in the Air Lines

With the exception of those leaves harvested after 12 hr. of continuous darkness, but including those gathered after 16, 20 and 24 hr. of continuous darkness, the air lines of all the quarters are similar to those described earlier (9) during the first six hours after harvesting. This normal type of air line is

shown for the purpose of comparison in Fig. 3. Fig. 4 shows a typical air line of leaves harvested after 12 hr. of darkness. This figure shows the peculiar behavior of the air lines of the third and fourth quarters to be called the "darkness hump". This peculiarity consists of an increase in the rate of oxygen uptake following gathering. It is absent, or almost absent, from the

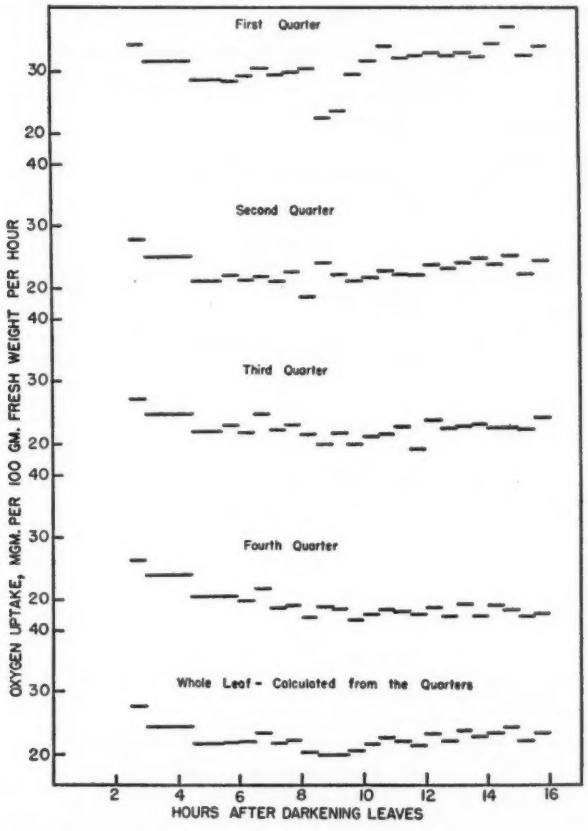

FIG. 3. The respiration record of the quarters of wheat leaves gathered after 12 hr. of continuous illumination.

records of all the tip quarters examined. Fig. 4 also shows that the respiratory rate of Quarter 1, after a three to four hour delay period, and to a progressively smaller extent and after a longer delay, of Quarters 2 and 3, rises slowly and steadily. Comparison with the Pettenkofer records in the files of Duff and Forward* shows that this rise is not a transpositional hump but the senescent

* *Personal communication.*

rise which sets in almost immediately after isolation in the case of leaves which contain very little sugar. As will be seen from Table IV, leaves produced under standard conditions contain practically no sugar after 12 hr. of continuous darkness. The more rapidly rising rates in the air lines of the upper quarters, setting in after the stimulatory decline, are doubtless associated with their greater protein content as explained previously (9) in the case of the senescent hump of standard leaves.

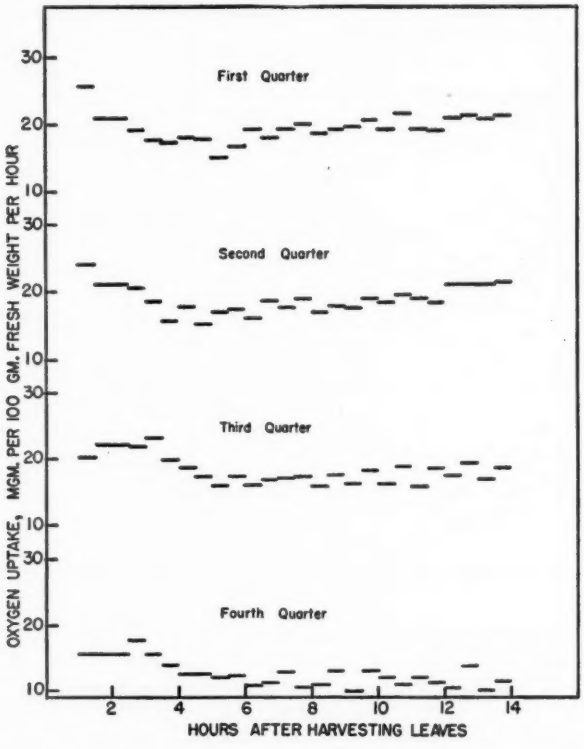

FIG. 4. The respiration record of the quarters of wheat leaves harvested after 12 hr. of continuous darkness.

Changes in the Gradient of Water Content

Figs. 5 and 6 present the data on the water contents of the 13-day-old first leaves of wheat after varying periods of light and darkness. It is generally true that the water content of the leaves decreases, as would be expected, during the period of illumination, and increases during the period of darkness. It is surprising that an increase in the water content occurs after eight hours of illumination. No explanation of this occurrence can be offered at present.

The diurnal variations in the water content of the tip quarter are greater than those of the second quarter, which in turn are greater than those in the third quarter, which are also greater than those in the fourth quarter. All these features would be expected in the leaves, if it is borne in mind that all the water enters the leaf at the basal end but transpires from the entire surface.

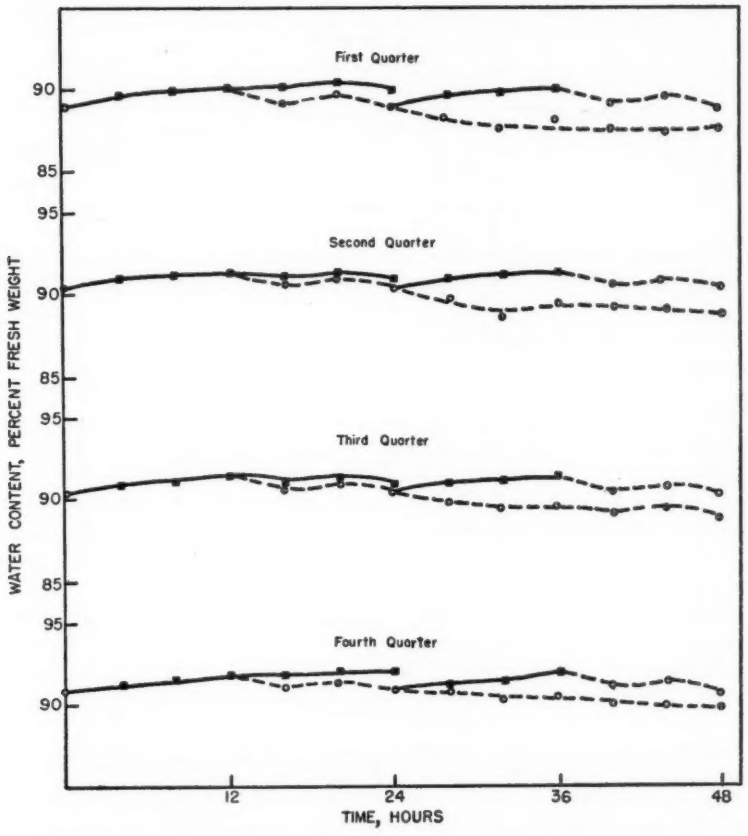

FIG. 5. Diurnal changes in the water content of the quarters of wheat leaves. The solid lines represent the periods of darkness, the broken lines the periods of illumination. The zero hour represents the close of the period of illumination at the end of the 12th day after planting. The graphs also show the course of the changes in water content if the period of darkness or illumination is prolonged beyond the normal period of 12 hr.

Fig. 6 shows the water content gradients in the leaves. Regardless of the period of illumination, at least within the limits tested, there is a water content gradient in the leaves from the base to the tip, with the greatest water content in the basal quarter of the leaf. In spite of appreciable changes

in the water content, this gradient persists little changed in magnitude. This gradient is probably the result of the basal quarter of the leaf being nearer to its water supply than is the tip quarter.

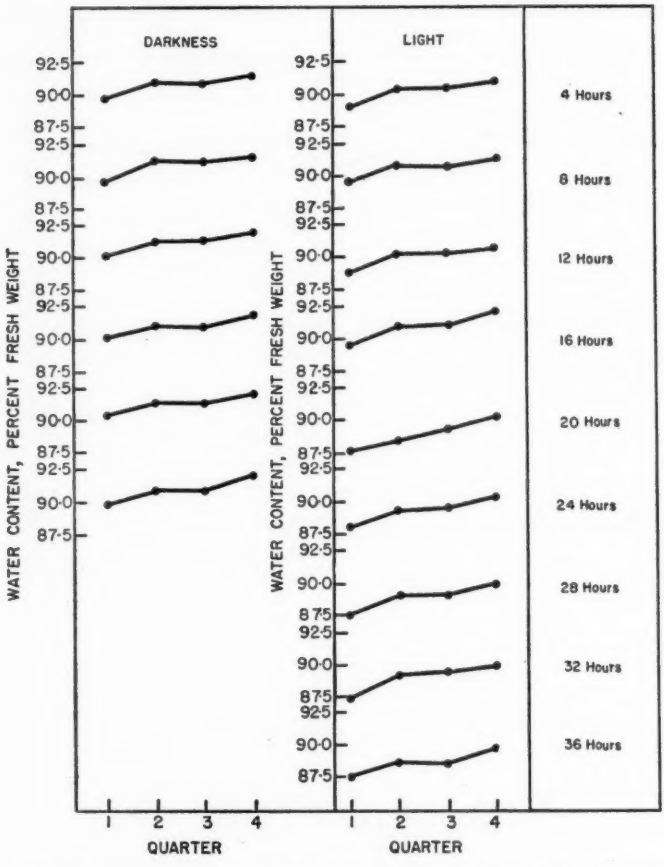

FIG. 6. The water content gradients in wheat leaves harvested after various periods of darkness or illumination.

Changes in the Gradient of Nitrogenous Substances

Table I gives the data on the protein nitrogen content of the leaves and quarters calculated on the basis of fresh weight. The data, when recalculated on the basis of dry weight show slightly less pronounced gradients than are shown by the figures in Table I. There is no indication from the data of a marked diurnal variation in the protein content of the leaves. The values for

TABLE I

THE CHANGES IN PROTEIN NITROGEN CONTENT INDUCED BY VARIOUS EXPOSURES TO LIGHT AND DARKNESS

Illumination before harvest	Protein nitrogen content as per cent fresh weight for:				
	Quarter 1	Quarter 2	Quarter 3	Quarter 4	Whole leaf
12 hr. light	.420 .433	.352 .379	.301 .308	.231 .258	.338 .349
8 hr. darkness	.397	.373	.341	.251	.341
12 hr. darkness	.419	.383	.347	.250	.355
22 hr. darkness	.445	.412	.380	.336	.392

protein nitrogen do appear to rise slightly after prolonged darkness, but it is possible that this is due to slight differences in cultural conditions as suggested below.

Table I shows that there is a pronounced protein gradient in the leaves from the tip to the base with the greatest concentration of protein in the tip quarter. This gradient does not change during the normal day period under our conditions of culture, nor does it undergo any change to correspond with the change in the respiratory gradient which occurs after prolonged periods of darkness. This point lends support to the view that the entire protein content does not wholly control the respiratory gradient. This must not be taken to mean that the concentrations of specific proteins may not control the gradient since this is probably the case.

Table II presents the data relevant to the diurnal changes in the soluble nitrogen content of wheat leaves. The data show that there is little or no diurnal change in the total soluble nitrogen content of wheat leaves under the conditions of culture outlined in the section on methods. The sample grown

TABLE II

THE CHANGES IN SOLUBLE NITROGEN CONTENT INDUCED BY VARIOUS EXPOSURES TO LIGHT AND DARKNESS

Illumination before harvest	Soluble nitrogen content as per cent fresh weight for:				
	Quarter 1	Quarter 2	Quarter 3	Quarter 4	Whole leaf
12 hr. light	.160 .175	.222 .191	.251 .232	.257 .242	.220 .207
8 hr. darkness	.158	.222	.249	.242	.220
12 hr. darkness	.164	.198	.231	.240	.206
22 hr. darkness	.219	.299	.346	.172	.255

for the experiment after 22 hr. of darkness was grown at a different time from the other samples and it is possible that slight differences in the water relations of the plant, especially due to humidity differences, are responsible for the higher nitrogen content of this sample. A drop in the humidity would cause the soil moisture to fall under my conditions of culture and this would increase the nitrogen content of the plants (6). Although there is no diurnal variation in the total soluble nitrogen content of the leaves, this does not mean that the content of nitrate and amino nitrogen does not vary diurnally. Any of the soluble nitrogenous constituents may vary diurnally but all of these diurnal variations must be compensated for by opposite variations in the other nitrogenous compounds.

The data, whether calculated on the basis of fresh or dry weight, show that there is a strong gradient in soluble nitrogen in the leaves from the base to tip, with the most nitrogen in the basal quarter. This gradient does not vary diurnally. The possible relationship of this gradient to the respiratory gradient is obscure. The behavior and configuration of this gradient does not suggest any direct relationship.

Changes in the Gradient in Reducing Substances

The data in Table III indicate the diurnal changes in the content of reducing substances in the leaves and their quarters. As mentioned earlier, the greater portion of these substances is probably not free reducing sugar. The identity of the reducing substances is unknown but it is suspected that part of them

TABLE III

THE CHANGES IN REDUCING SUBSTANCE CONTENT CALCULATED AS GLUCOSE INDUCED BY VARIOUS EXPOSURES TO LIGHT AND DARKNESS

Illumination before harvest	Reducing substances as glucose, % fresh wt. in:									
	Quarter								Whole leaf	
	1		2		3		4			
	H*	S**	H	S	H	S	H	S	H	S
12 hr. light	.27	.17	.18	.09	.16	.06	.14	.07	.19	.11
	.26	.18	.16	.09	.13	.06	.09	.06	.16	.09
24 hr. light	.26	.17	.15	.10	.14	.09	.10	.06	.16	.11
	.74	.48	.54	.38	.47	.33	.35	.27	.54	.38
12 hr. darkness	.36	.20	.17	.06	.15	.04	.08	.02	.20	.19
	.46	.31	.16	.10	.13	.04	.00	.02	.18	.12
24 hr. darkness	.18	.07	.14	.04	.12	.03	.09	.01	.14	.03
	.29	.13	.16	.05	.13	.04	.07	.07	.17	.07

* *H* = *These values obtained by Hanes method (3).*
** *S* = *These values obtained by Somogyi method (10).*

represent degradation products of ascorbic acid. The data do not show any definite pattern of changes with changed periods of illumination prior to harvest. There is evidence that considerable differences may occur in the reducing substance content of the leaves. No reason for the great difference in sugar and reducing substance content between the two samples subjected to 24 hr. of continuous illumination prior to harvest is known.

The data do show that there is a strong gradient in reducing substance content from tip to base of the leaves, with the largest quantities of the reducing substances in the tips of the leaves. The gradient in these substances does not show any pronounced change after a long period of darkness that might correspond to the change observed in the respiration gradient after such treatment. It is unlikely, therefore, that the distribution of these substances is directly responsible for the gradient in oxygen uptake in the leaves which was described earlier.

Changes in the Gradient of Sucrose

The data on sucrose distribution in the leaves, presented in Table IV, show very clearly the diurnal variations in the sucrose content of the leaf tissues. Sucrose increases in the leaves in the light and decreases in the dark. Diurnal variations in sucrose content are usually found in leaves. Since newly isolated wheat leaves contain little or no free reducing sugar (7), it is apparent that the first carbohydrate-like product of photosynthesis to accumulate in the leaves is sucrose. If the sucrose is formed from free reducing sugars, they must be present as transitory intermediates in the synthesis of sucrose in quite low concentrations. From a comparison of the sucrose contents of the quarters after 12 and 24 hr. of illumination, it can be seen that the rate of accumulation of sucrose has decreased with prolonged exposure to light. This may be due to an increased rate of translocation of sucrose out of the leaves, or to a reduction in the rate of photosynthesis. More data on the sugar contents at shorter time intervals, and data on the sugar contents of the leaf sheaths, would be needed to settle this point. The tables also show that almost all the sugar has been removed from the leaves after 12 hr. of darkness. It appears that traces may be present in the leaves even after 20 or more hours of darkness.

With the exception of one of the samples taken after 24 hr. of light, all those which contained detectable quantities of sucrose showed a strong gradient in sucrose from the tip to the base of the leaves, with the greatest concentration of sucrose in the tip quarters. This gradient shows a much greater regularity and persistence than does the gradient in oxygen uptake.

One of the samples gathered after 24 hr. of illumination contains very high sugar concentrations and a different gradient from the other samples. The causes of these differences in this sample are unknown.

TABLE IV

CHANGES IN SUCROSE CONTENT INDUCED BY VARIOUS EXPOSURES TO LIGHT AND DARKNESS

Illumination before harvest	Method used*	Sucrose as per cent fresh wt. in:				
		Quarter				Whole leaf
		1	2	3	4	
12 hr. light	H	.91	.70	.57	.49	.69
	S	.98	.72	.60	.31	.62
	I	.91	.72	.62	.39	.63
	F	.82	.50	.35	.13	.47
12 hr. light	H	.84	.82	.61	.37	.68
	S	.93	.87	.62	.38	.72
	I	.93	.80	.60	.37	.70
	F	.72	.69	.42	.17	.53
24 hr. light	H	1.35	.93	.79	.52	.93
	S	1.42	1.11	.80	.54	.98
	F#	1.01	.89	.82	.51	.82
24 hr. light	H	1.54	1.20	1.47	1.04	1.32
	S	1.60	1.48	1.44	.88	1.36
	I	1.16	1.22	1.64	1.23	1.30
	F#	1.43	1.41	1.43	1.14	1.35
12 hr. darkness	H	.27	.10	.10	.05	.22
	S	.00	.03	.16	.04	.07
	I	.21	.00	.00	.00	.05
	F	.10	.00	.00	.00	.03
12 hr. darkness	H	.24	.10	.09	—	—
	S	.00	.00	.00	.00	.00
	I	.18	.04	.00	.00	.05
	F	.40	.09	.00	.00	.12
21 hr. darkness	H	.10	.07	.05	.03	.07
	S	.00	.00	.00	.00	.00
21 hr. darkness	H	.12	.08	.04	.03	.07
	S	.00	.00	.00	.00	.00

* *H* = *Values obtained by Hanes' method after acid hydrolysis.*
S = *Values obtained by Somogyi's method after acid hydrolysis.*
I = *Values obtained by Somogyi's method after invertase hydrolysis.*
F = *Values obtained by a modification of Roe's method (see 7) on the assumption that the leaves contain no free fructose.*
F# = *Values obtained by the same method as in F except that no correction was applied for interfering substances.*

Discussion

Having described the experimental results it now remains to consider the possible basis of the observed physiological heterogeneity in the leaves. Further consideration will be given to this question in a later paper on the effects of soil moisture upon the heterogeneity in the first leaf of wheat.

Regular diurnal changes have been found to occur in the respiratory rate of each of the quarters of the first leaf but there are no corresponding changes in the protein or soluble nitrogenous fractions of the leaves or in the reducing substances in the leaves. Although there are pronounced changes in the sucrose content of the seedling leaf diurnally these changes are proportionately very much greater than the corresponding changes in the respiratory rate. These results show that the respiratory rate of the first leaf of wheat is not controlled diurnally by the concentrations of sucrose, reducing substances, or protein.

When attention is directed toward the gradient in the first leaf similar conclusions are reached. There is considerable variability in the respiratory gradient in the leaves. One of the most striking features of this gradient is the steep gradient which develops after 16 hr. of darkness. There is no corresponding change in the protein soluble nitrogen, reducing substance, sucrose or water content gradients. In fact the gradients of the different chemical constituents of the leaves show a very pronounced stability in contrast to the great variability of the respiratory gradient.

The existence of the "darkness hump" in the air lines after 12 hr. of continuous darkness suggests that probably the heterogeneity has a complex basis. It seems quite unlikely that this phenomenon will be explained until much more is known about the complicated machinery of respiratory metabolism.

During some of the exploratory experiments, a gradient in chlorophyll in the leaves was clearly indicated. When equal weights of the different quarters were allowed to stand overnight in 80% alcohol the intensity of the green color in the liquid next day showed a strong gradient in chlorophyll with the greatest quantities in the tip quarter and least in the basal quarter. This same phenomenon was apparent in the alcohol extraction of the sugars from the quarters.

The gradient in chlorophyll suggests that there is an anatomical gradient in the leaves with the most chlorenchyma in the tip of the leaf and least in the basal portion. Since a large part of the proteinaceous material in leaves is considered to be associated with the chloroplasts (5) the idea of an anatomical gradient fits in well with the demonstrated protein gradient. If we assume that a chlorophyll gradient indicates a gradient in photosynthetic machinery then it would be expected that most sucrose would accumulate in the place where there is most photosynthetic machinery. This is what is observed.

Leaf anatomy probably enters into the problem of leaf heterogeneity in a second way. The general construction of the leaf is such that water and dissolved materials (other than those present in the atmosphere) must enter or leave the leaf only at the basal end whereas there is free gas exchange with the atmosphere along the entire surface of the leaf. These anatomical arrangements likely account for the gradient in water content observed in the leaf. They could account for the sucrose gradient observed in the leaf during

the period of illumination and they probably contribute to the maintenance of this gradient together with the greater quantity of chlorophyll in the tip section of the leaf.

The problem of anatomical heterogeneity of the leaf and its consequences will be considered further in later papers in the present series. The data presented above suggest that it is an important factor in the physiological heterogeneity of the first leaf of Khapli Emmer wheat.

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STUDIES ON THE PERFECT STAGE OF *HELMINTHOSPORIUM SATIVUM*[1]

By R. D. Tinline[2]

Abstract

Cochliobolus sativus, the perfect stage of *Helminthosporium sativum*, developed in some paired cultures of monoconidial isolates. A satisfactory medium for the propagation of perithecia consists of kernels of barley placed on Sach's nutrient agar. The barley was prepared by surface sterilization, followed by boiling to kill the embryos. Cultural studies of monoascosporic isolates showed that the fungus is heterothallic in the sense that the isolates are hermaphroditic, self-sterile, intragroup sterile, and intergroup fertile. The change from a conidial to a mycelial-type colony in one isolate was shown to be a true mutation. The two compatibility groups in *C. sativus* were shown to be randomly distributed in nature. Isolates of the fungus from any one area were observed to fall into either compatibility group. A comparison of the author's *C. sativus* with the description of *Ophiobolus sativus* given by Ito and Kuribayashi led to the conclusion that these fungi are identical.

Introduction

Helminthosporium sativum P. K. & B. is a well known pathogen of cereals. Although it has been studied extensively, there have been but two reports of its ascigerous stage. Ito and Kuribayashi, in 1929, described an ascigerous fungus obtained in culture as the perfect stage of *H. sativum* under the binomial *Ophiobolus sativus* (P.K. & B.) Ito & Kurib. Kuribayashi (12)). In 1949, Tinline, Sallans, and Simmonds (14) reported the production of perithecia in paired monoconidial cultures of *H. sativum*. It is the opinion of the author that the *O. sativus* published by Ito and Kuribayashi and the perithecial stage of *H. sativum* reported by Tinline *et al.* are identical.

In 1934, Drechsler (7) erected the new genus *Cochliobolus* to include the helicoid ascigerous species, with conidia belonging to *Helminthosporium*, that had previously been referred to the genus *Ophiobolus*. He based his new genus on *Ophiobolus heterostrophus* Drechsler (6), but did not specifically transfer *O. sativus* to the new genus. However, in 1942, Dastur (3) attributed the transfer to him, using the binomial *Cochliobolus sativus* (Ito & Kurib.) Drechsler. Accordingly, in Review of Applied Mycology, Supplement 12, page 133, 1946, the full authority for *C. sativus* is given as (Ito & Kurib.) Drechsler ex Dastur. For these reasons, the perfect stage of *Helminthosporium sativum* discussed in this paper will be referred to *C. sativus*.

In 1942, Dastur (3) obtained an ascigerous fungus which he considered to be generically similar to *C. heterostrophus* and *C. sativus*, but specifically distinct from them. He named it *C. tritici* n. sp. No further information is available concerning this species.

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The present paper gives an account of studies on the production of perithecia in *C. sativus*, especially as influenced by cultural conditions; some observations on the morphology and life history of the fungus; and evidence of its heterothallic nature. Monoconidial isolates have been used throughout these studies. The author has assumed that when single conidia are used for cultures, the genotypes of the cultures are the same as those of the original conidia, unless mutation occurs. Christensen and Davies (2) concluded that most young conidiophores of *H. sativum* (*C. sativus*) are uninucleate. Consequently, the nuclei of a conidium are derived from one nucleus.

Culture Methods

Fifty-six monoconidial isolates of *C. sativus* were obtained from diseased plants collected in the same number of different localities in Saskatchewan. The isolates were cultured upon potato dextrose agar in test tubes. In order to devise a satisfactory method of producing perithecia of this fungus in culture, a wide variety of natural and artificial media were tried, including such materials as sterilized straw of cereals and grasses, wheat seedlings, and cereal seed, and in addition, artificial media to which certain vitamins were added. The isolates were grown in pairs, as well as singly, on the various media employed.

Sterilized Straw

The 56 isolates were divided into sets of four. Conidia from each of the four isolates of a set were transferred to one tube of sterile water to make a suspension of mixed inoculum. Inocula from five such sets of isolates were thus prepared. All of the 10 possible pairings of the five sets of inoculum were made, each pairing of two sets embracing eight isolates. Mature wheat straws were cut into lengths of from two to three inches and placed in other test tubes, several such lengths to a tube. To each tube were added a few cubic centimeters of distilled water. After steam sterilization, the tubes were inoculated with different suspensions of conidia. A second and a third test, embracing 20 isolates and 16 isolates respectively, were set up in a similar manner. The tests were conducted in quintuplicate. Since no information was available on the conditions favoring the production of perithecia in *C. sativus*, trials to produce the perfect stage were conducted under a variety of conditions. The conditions under which the replicates were placed were: (*a*) room temperature, approximately 22° C., with ordinary room lighting, (*b*) room temperature, with direct sunlight, (*c*) room temperature, with light excluded, (*d*) temperature of approximately 25° C., with diurnal variations of light, and (*e*) out of doors for four weeks, with temperature fluctuations between 5° and 27° C., followed by a three week period at room temperature, with ordinary room lighting.

Two or three weeks after the inoculations, small black perithecium-like bodies, later shown to be perithecial primordia, were observed in some of the tubes that had been placed in a darkened cabinet at room temperature.

Although mature perithecia did not develop, the presence of these primordia indicated that, under the proper conditions, the perfect stage might be expected to develop in pure culture.

It may be mentioned here that, in this and later tests, room temperature and high humidity were found to be the conditions under which the most satisfactory development of perithecia took place. Light appeared to be an unimportant factor.

The eight isolates of those sets which had produced perithecial primordia in culture, were transferred singly, and in all possible pairs, to sterilized straw in test tubes. Two isolates when grown singly, and four of the pairs of isolates, produced perithecial primordia. The primordia of three of these four pairs developed into perithecia containing asci and ascospores. No asci developed in any of the cultures of single isolates. The isolates, four in all, which when cultured in pairs produced perithecia, shall for the purpose of this paper be referred to as "fertile" isolates, merely to identify them, and without regard to their compatibility.

Frequently "fertile" isolate pairings on sterilized wheat straw failed to produce perithecia. Consequently sterilized straw other than wheat straw was tried. Of the cereal straw tested as a medium for the production of perithecia, barley was better than wheat, oats, or rye—in descending order. Straw of indigenous or cultivated grasses also was tested, but only that of four species, namely, *Hordeum jubatum*, *Agropyron cristatum*, *A. pauciflorum*, and *Poa* sp., supported the development of perithecium-like bodies, and of these bodies only those that developed on the straw of *Poa* sp. contained asci and ascospores.

Although some of the different straw material mentioned above occasionally supported the development of perithecia, straw proved generally unsatisfactory as a medium, and other materials were explored.

Seedlings

Wheat seeds, surface sterilized with mercuric chloride solution (1 : 1000) were placed on moist filter paper in Petri dishes. The seeds were inoculated with single and paired "fertile" isolates of *C. sativus*. A drop of a suspension of conidia from cultures of these isolates was transferred to each seed by means of a small glass rod. Some seedlings bearing lesions were obtained from the inoculated seeds, and these were placed on Sach's nutrient agar in large test tubes. In this and later tests the reaction of Sach's nutrient agar was adjusted to approximately pH 6.5 by the addition of calcium carbonate prior to steam sterilization. In four or five weeks the seedlings were killed by the fungus. These seedlings were removed from the tubes and examined closely. Black perithecium-like bodies, a few of which contained asci and ascospores, were found inside some of the empty seed coats. When Petri dishes containing seedlings arising from seed similarly inoculated, and incubated for several weeks, were examined, numerous small perithecium-like bodies were found present on the roots of the seedlings. None of these bodies developed asci.

Vitamins in the Media

Some fungi are incapable of synthesizing certain growth-promoting substances necessary for reproduction and other physiological processes. Certain vitamins were, therefore, incorporated into the media used in some of the tests designed to induce the development of the perfect stage of *C. sativus*.

Biotin, thiamine, riboflavin, and calcium pantothenate were added to Sach's nutrient agar on which surface-sterilized wheat and barley seedlings were placed. Some of the seedlings were boiled to prevent further growth. The seedlings were inoculated with suspensions of conidia of "fertile" isolates. Perithecial primordia developed in all cultures of single isolates. Perithecia containing asci developed in some cultures of paired isolates. No significant differences were observed, however, between the numbers of primordia or perithecia propagated in the cultures containing vitamins and those which did not contain vitamins.

Bran agar, corn meal agar, potato dextrose agar, and Sach's nutrient agar, on which single and paired "fertile" isolates were grown, failed to support the development of perithecial primordia or perithecia, regardless of the presence or absence of the vitamins.

The results to this point indicated that some substances present in cereal seed and to some extent in cereal straw were essential for the development of perithecia, whereas the addition of vitamins was not essential. Consequently, attention was given to cereal seed as a medium.

Boiled Seed

Surface-sterilized wheat seed was inoculated with the conidia of single and paired monoascosporic cultures and placed on Sach's nutrient agar in test tubes. In this and all later tests, unless otherwise stated, the inoculum was prepared by transferring the conidia of the cultures to a small quantity of sterile water. Inoculation of the seed was accomplished by immersing the seed in the inoculum. Perithecial primordia developed only on the ungerminated seeds but not on the seedlings that arose from some of the sterilized seed.

A further test substantiated the above results. Surface-sterilized wheat seed, half of which had been killed by boiling for two or three minutes, was inoculated with paired "fertile" isolates. The seed was placed on Sach's nutrient agar in Petri dishes. Perithecia developed profusely on the boiled seed, whereas no perithecia developed on the seedlings arising from the seed which was not boiled.

In supporting the development of perithecia on inoculated, boiled wheat seed, Sach's nutrient agar was found to be much superior to either potato dextrose agar or Westergaard and Mitchell's medium (15). The two latter favored the development of conidia, whereas Sach's nutrient agar suppressed it, and favored the formation of perithecia. For the examination of the cultures, the covers of the Petri dishes had to be frequently removed, thus exposing the media to air-borne contaminants. The Sach's agar remained free from the

growth of these contaminants much longer than the other media, a result probably due to its low concentration of carbohydrates. This characteristic facilitated the examination of the cultures.

Nine isolates which had failed to produce primordia or perithecia on rye straw or pieces of corn stalks, were retested for their ability to produce perithecia on other media. In addition, three "fertile" isolates were included in this test. Twelve plates of Sach's nutrient agar were poured. Wheat seed, surface-sterilized with mercuric chloride and boiled to kill the embryos, was placed on the agar, 12 seeds per plate. Suspensions of conidia, one for each isolate, were prepared. The seed was inoculated with single and paired isolates of the fungus, by applying a drop of a suspension, or of a mixture of two suspensions, to the seed. Although asci were not observed, numerous perithecial primordia arose from almost all these inoculations. Likewise, cultures derived from ascospores and asci, when grown on boiled barley seed plated on Sach's agar, produced perithecial primordia without fail. Of wheat, oat, barley, and rye seed, all surface sterilized, killed by boiling, inoculated, and plated on Sach's agar, barley seed was the most successful medium for the development of perithecia.

Four methods of sterilizing and killing barley seed were tested to determine to what extent they influenced the production of perithecia. The seed was (*a*) boiled in sterile water for five minutes; (*b*) soaked in tap water for 30 min., drained, and the container with the seed was plugged and autoclaved for 20 min.; (*c*) immersed in mercuric chloride for five minutes, washed with three changes of sterile water, and boiled for two or three minutes to kill the embryos; (*d*) immersed in mercuric chloride for five minutes, drained, covered with a 10% solution of sodium sulphide for five minutes in order to precipitate the mercury, then washed with three changes of sterile water, and finally boiled for two or three minutes. Seed from each treatment was inoculated with the fungus and plated on Sach's agar. Examinations disclosed that perithecia were much more numerous on those seeds that had been sterilized by methods (*c*) and (*d*) than on seeds treated by the other methods.

Nine additional monoconidial isolates of *C. sativus* were obtained from wheat stubble. The isolates were paired with each of two "fertile" isolates and cultured on barley seed placed on Sach's agar. One pair of isolates was especially "fertile" in that this pair produced numerous perithecia containing asci and ascospores. From repeated tests, equally successful, many single ascospores were isolated. Cultures arising from these ascospores always produced typical *C. sativus* conidia. Periodic examinations of 25 of these monoascosporic cultures on potato dextrose agar disclosed no cultural differences between the colonies. The inoculation of wheat seedlings with these cultures produced on the coleoptiles lesions characteristic of infection by *C. sativus*. The conidial stage of the fungus was readily reisolated from the lesions.

Heterothallism

The culture work reported above suggested that *Cochliobolus sativus* is heterothallic: perithecia were produced only when monoascosporic or monoconidial isolates were grown in pairs; single monoascosporic or monoconidial isolates produced only perithecial primordia, or none at all.

To clarify this situation, two tests were conducted. Twelve monoascosporic isolates in the first test, and nine in the second, were grown singly and in all possible pairs. All the monoascosporic isolates originated from perithecia produced by a single pairing of two monoconidial isolates. The results of these tests are presented in Figs. 1 and 2, respectively. The criterion of fertility, i.e., the development of perithecia, is the production of asci. Though all the squares of Figs. 1 and 2 are completed, the data are based on pairings and not on reciprocal crosses of the isolates.

Fig. 1 shows that the 12 isolates represent two distinct compatibility groups, one group, designated as *A*, consisting of isolates 12, 14, 20, and 22, and the other group, designated as *a*, consisting of isolates 11, 13, 15, 16, 17, 18, 19, and 21. These groups exhibit intragroup sterility and intergroup fertility.

	11	13	15	16	17	18	19	21	12	14	20	22
11	−	−	−	−	−	−	−	−	+	+	+	+
13	−	−	−	−	−	−	−	−	+	+	+	+
15	−	−	−	−	−	−	−	−	+	+	+	+
16	−	−	−	−	−	−	−	−	+	+	+	+
17	−	−	−	−	−	−	−	−	+	+	+	+
18	−	−	−	−	−	−	−	−	+	+	+	+
19	−	−	−	−	−	−	−	−	+	+	+	+
21	−	−	−	−	−	−	−	−	+	+	+	+
12	+	+	+	+	+	+	+	+	−	−	−	−
14	+	+	+	+	+	+	+	+	−	−	−	−
20	+	+	+	+	+	+	+	+	−	−	−	−
22	+	+	+	+	+	+	+	+	−	−	−	−

FIG. 1. Diagram showing the result of pairing 12 monoascosporic isolates of *H. sativum*, all originating from perithecia produced by a single pairing of two monoconidial isolates. In this, as well as in Figs. 2 and 3, the symbol + indicates that perithecia developed, and the symbol − that perithecial primordia only developed.

The mechanism of fertilization in *C. sativus* is not known and no evidence was obtained of any differentiated male structures. The production of perithecial primordia by a haploid isolate has been accepted as an attribute of the female character, following the lead of Hansen and Snyder (8). There is evidence that the isolates of at least one of the two groups mentioned must be hermaphroditic, or monoecious. Each of the 12 isolates produced perithecial primordia, a feature indicative of femaleness; and, as the two groups

are interfertile, at least the isolates of one group, if not of both, must possess maleness as well. Further, each of the isolates is self-sterile, as none of them develop perithecia when grown alone.

The results of the second test (Fig. 2) confirm that the isolates are hermaphroditic, self-sterile, intragroup sterile, and intergroup fertile.

	27	29	30	32	34	28	31	33	35
27	−	−	−	−	−	+	+	+	+
29	−	−	−	−	−	+	+	+	+
30	−	−	−	−	−	+	+	+	+
32	−	−	−	−	−	+	+	+	+
34	−	−	−	−	−	+	+	+	+
28	+	+	+	+	+	−	−	−	−
31	+	+	+	+	+	−	−	−	−
33	+	+	+	+	+	−	−	−	−
35	+	+	+	+	+	−	−	−	−

FIG. 2. Diagram showing the result of growing nine monoascosporic isolates, of the same origin as the 12 isolates of Fig. 1, singly, and in all possible pairs.

To correlate the groups *A* and *a*, shown in Fig. 1, with the groups shown in Fig. 2, four isolates, one from each group of each test, were cultured in all possible pairs. It was found that isolates 27, 29, 30, 32, and 34 were of compatibility group *A*, and isolates 28, 31, 33, and 35 were of compatibility group *a*. Therefore, of the 21 monoascosporic isolates tested, nine belonged to group *A*, and 12 to group *a*.

Additional evidence of the hermaphroditic nature of the fungus was obtained by the apparent mutation of one of the monoascosporic isolates. Isolate 19, for some time, was similar to the other 11 isolates shown in Fig. 1, when they were grown on potato dextrose agar. The colonies were black in color, and conidia were developed in profusion by all of them. Perithecial primordia were produced under favorable conditions by each of the 12 isolates. After several months, however, subcultures of isolate 19 appeared morphologically distinct from those of the other isolates. The mutant produced few conidia and abundant mycelium, the colony being light gray rather than black. No perithecial primordia were produced by the mutant in single cultures. Perithecia were formed, however, when the mutant was paired with an isolate of the opposite compatibility group. Hence it is apparent that the original isolate 19 was a hermaphrodite, for although the factor for the development of perithecial primordia, i.e., femaleness, was lost, the factor for maleness must have been retained.

The change of isolate 19 from a conidial to a mycelial type was found to be a true mutation. Three ascospores were isolated from a single ascus of a perithecium which arose as the result of pairing the mutant from isolate 19 with a conidial type isolate of the opposite compatibility group. When grown on potato dextrose agar, two of the ascospores produced typical conidial type

colonies, whereas the remaining ascospore produced a mycelial type colony similar to that of the mutant parent.

The mutation of isolate 19 from the conidial to the mycelial type appears to be an example of the "dual phenomenon" described by Hansen and Snyder (8). These workers postulated that in *Hypomyces solani* f. *cucurbitae* the mutation from the conidial to the mycelial type was in effect a mutation from the hermaphroditic to the unisexual male condition. The mutation of isolate 19 of *C. sativus* conforms to this theory. Miss Hirsch (9), from a cytogenetic study of sex, was able to explain the mutation in *H. solani* of a hermaphrodite to a unisexual male. This mutation involved the loss of an entire chromosome.

Further evidence that the phenomenon of self-sterility, intragroup sterility, and intergroup fertility is characteristic of *C. sativus*, was obtained in the following way. Fourteen monoconidial isolates were made from naturally infected seed obtained from an equal number of widely distributed localities in Canada and the United States. Four additional monoconidial isolates were obtained from diseased seedlings in Saskatchewan. The geographic distributions of the monoconidial isolates are as follows: M_1, M_2, M_3, M_4,—New Brunswick; B_9—Quebec; N_5—Nova Scotia; W_3, W_4, W_5, W_6,—Wisconsin; O_5—Ontario; D_1, D_2,—Manitoba; S_1, S_2, S_3, S_4, S_5,—Saskatchewan.

Each of the 18 monoconidial isolates was grown singly, and also paired with each of two monoascosporic isolates, 18 and 22, of compatibility groups *a* and *A*, respectively.

The results of the test, presented in Fig. 3, show that the monoconidial isolates are self-sterile, intragroup sterile, and intergroup fertile. Nine isolates, namely M_1, M_2, B_9, N_5, W_3, O_5, S_1, S_2, and S_4, belonged to compatibility group *a*; the other nine isolates, M_3, M_4, W_4, W_5, W_6, D_1, D_2, S_3, and S_5, to compatibility group *A*.

	M1	M2	B9	N5	W3	O5	S1	S2	S4	M3	M4	W4	W5	W6	D1	D2	S3	S5
0	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
18	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+	+	+
22	+	+	+	+	+	+	+	+	+	−	−	−	−	−	−	−	−	−

FIG. 3. Diagram showing the result of growing each of 18 monoconidial isolates singly, and in pairs, with each of two monoascosporic isolates, 18 and 22, of compatibility groups *a* and *A*, respectively.

Not only did all the isolates separate into two compatibility groups, but isolates from single geographic locations, namely New Brunswick, Wisconsin, and Saskatchewan, likewise segregated into the two groups *a* and *A*.

Description of the Ascigerous Stage

The morphological characteristics of the perfect stage of *Cochliobolus sativus* growing in pure culture were studied. These characteristics were similar to those described by Ito and Kuribayashi (Kuribayashi (12)) for their fungus.

In cultures arising from inoculated seed placed on Sach's nutrient agar, perithecia first appear within from 4 to 10 days as white to yellow-brown tufts or mats of mycelia, either on the seed (often superficially) or in the agar near the seed. Upon microscopic examination, they were found to consist of hyaline pseudoparenchymatous cells and mycelium. Some of these structures became arrested at this stage of development, others increased in size until the end of the fourth or fifth week, during which time the color changed from white to brown to black. Perithecia three or four weeks old usually yield, upon crushing, numerous immature asci, among slender, massed paraphyses. Later, when the fruit bodies are examined, few to numerous asci and ascospores in all stages of development are clearly visible (Figs. 5 and 7). As many as 60 asci have been observed from a single perithecium.

Mature perithecia are erumpent from the dead host tissue, or superficial or immersed in the agar media (Fig. 4). They are pseudoparenchymatous, fragile, black in color, and usually beaked (Fig. 8). Externally, the perithecia are sparsely covered with setae, conidiophores, and conidia. Beaks are variable in size, and are subconical or paraboloid in shape. The ostiole may or may not be well defined, depending on the stage of maturity of the perithecium (Fig. 6).

Asci are thin-walled, cylindrical or clavate, straight or slightly curved, widest below the middle, short stipitate, with round apices, containing one to eight ascospores coiled in a close helix (Fig. 9). As in *C. heterostrophus* Drechsler (6), the rotation of the helix was found to be always in the same direction, i.e., reading from base to apex, on an upper focus, the coiling is from right to left. Also, as in that species, a mature ascus of *C. sativus* in a water mount discharges its spores simultaneously by the circumscissile rupture of the upper part of the ascus wall (Fig. 10). The ruptured apical portion often remains attached to the ascus wall after the liberation of the spores. That asci normally extrude through the ostiole is apparent from the examination of exudate collecting at the tips of the beaks of some perithecia. Paraphyses are present, very numerous, extremely slender, hyaline, changing to olivaceous in old cultures (Fig. 6). Apparently they decrease in number as the asci are formed.

Ascospores, upon escape from the ascus, gradually uncoil and become free (Fig. 11). They are filiform or flagelliform, hyaline, changing to olivaceous, granular, pointed at the extremities, few to many septate (Fig. 12). The ascospores germinate promptly by sending out one or more germ tubes from one to all segments, terminally or laterally (Fig. 13). Ascospores in old cultures often disarticulate into their component segments; each segment is capable of germination. Young ascospores are nonseptate but, if they are liberated and placed on agar, they become septate prior to germination. Ascospores are often capable of germinating *in situ* in the ascus when dehiscence fails to occur.

Although the asci usually contain four, six, or eight normal spores, occasionally there are present, besides several normal ascospores, one or more smaller structures which are probably undeveloped ascospores.

Measurements were made of the perithecia, asci, and ascospores of the fungus. These measurements are compared in Table I with the corresponding data given by Ito and Kuribayashi (Kuribayashi (12)) for *C. sativus*.

TABLE I

COMPARISON OF MEASUREMENTS OF PERITHECIA, ASCI, AND ASCOSPORES OF *Cochliobolus sativus*

	Perithecia	Ostiolar beak	Asci		Ascospores		Septa
			Length	Width	Length	Width	
Ito and Kuribayashi	370–530 × 340–470μ	90–150 × 80–110μ	110–220μ	32–45μ	160–360μ	6– 9μ	6–13
Author	310–460 × 270–420μ	66–190 × 90–140μ	160–255μ	27–42μ	182–343μ	5–10μ	6–14

Table I shows that the measurements obtained by the author are in general agreement with those given by Ito and Kuribayashi. Moreover, these two sets of measurements are more closely alike to each other than are, respectively, the measurements of other species of this genus. This comparison supports the claim, made at the beginning of the paper, that the perithecia described by Ito and Kuribayashi and those described by Tinline *et al.* (14) are identical. Although the measurements of the perithecia, asci, and ascospores, of the two authors generally agree, the slight differences that exist may perhaps be attributable to variant strains of the fungus, and environmental and cultural differences.

Discussion

The results of this investigation indicate that the growth of "fertile" isolates, i.e., two isolates of opposite compatibility groups, on a suitable medium is a prerequisite for the development of perithecia in *Cochliobolus sativus*.

The results of pairing monoascosporic isolates show that *C. sativus* is heterothallic in the sense that the isolates are hermaphroditic, self-sterile, intragroup sterile, and intergroup fertile. This type of heterothallism, sometimes referred to as monoecious heterothallism, is not new among the Ascomycetes, a few examples of which may be cited. Drayton (5) demonstrated the phenomenon of self-sterility and fertility only between certain isolates in *Sclerotinia gladioli*. Ames (1) showed that cultures from uninucleate ascospores of *Pleurage anserina* are bisexual, self-sterile, and cross-fertile. Keitt and Palmiter, and Keitt *et al.* (10, 11) concluded, and later confirmed, that *Venturia inaequalis* is heterothallic, each isolate being hermaphroditic and self-sterile. Hansen and Snyder (8) demonstrated monoecious heterothallism in *Hypomyces solani* f.

cucurbitae. Certain Ascomycetes produce both male and female structures on the same haploid thallus, as shown by Drayton (5) and Hansen and Snyder (8). Although in *C. sativus* male structures were not discernible as such, yet since monoascosporic isolates were shown to function both as males and females, the monoecious nature of the haploid thalli cannot be doubted. The process of fertilization in this fungus remains to be investigated.

It seems probable, from the results obtained, that the compatibility group factors of the fungus are segregated in a 1 : 1 ratio in nature.

One possible explanation of the nonobservance of the perfect stages in some species of *Helminthosporium* may be associated with monoecious heterothallism. Under such a phenomenon only certain pairings or crosses of the isolates of a species could propagate perithecia.

From the work reported in this paper, since the sexual stage of *C. sativus* described by Kuribayashi (12) and that described by the author are similar morphologically, and since both authors found the conidial stage of *C. sativus* to be *Helminthosporium sativum* P.K. & B., it is concluded that the fungi are identical.

Whether or not *C. tritici* is identical with *C. sativus*, as has been suggested by Dickson (4), is largely a matter of conjecture. Dastur (3) concluded from a comparison of his fungus with *C. sativus* that his fungus was sufficiently distinct morphologically to warrant a new specific name.

Perithecia of *C. sativus* would be expected to occur in the field whenever *A* and *a* haplonts happened to grow together. The presence of perithecia in the field, however, despite many years of study on the disease caused by this organism, does not appear to have been reported. The significance of such an occurrence is difficult to estimate. It may, however, explain the wide variation and the numerous physiologic forms so often observed in *C. sativus*. The wide dissemination of this cereal pathogen has been largely attributed to air-borne conidia. Stakman *et al.* (13) described numerous *Helminthosporium* conidia caught up to a height of 10,000 ft. Investigators doing spore-trap work in Saskatchewan also found some air-borne conidia of *C. sativus*. It seems likely that ascospores may play a part in dissemination. Their slender form may indicate good adaptation to dissemination by air.

Acknowledgments

The author is greatly indebted to Dr. B. J. Sallans for his valuable suggestions and assistance during the progress of the investigations. He also wishes to thank Dr. P. M. Simmonds and members of the staff for many helpful consultations and criticisms.

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NOTE: *Plates I and II follow.*

PLATE I

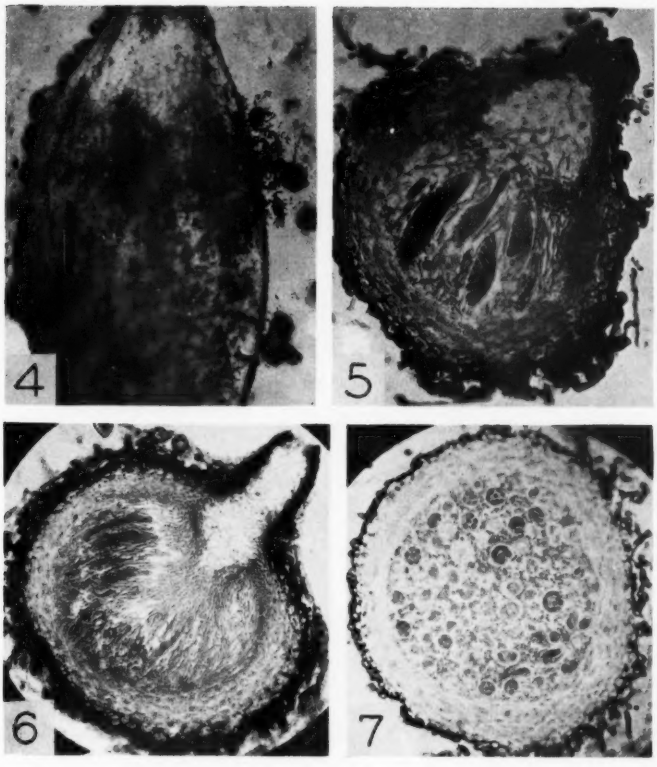

FIG. 4. Perithecia developing on and around a boiled barley seed plated on Sach's agar. × 10. FIG. 5. Longitudinal section of a perithecium showing the setose exterior of the pseudoparenchymatous peridium, asci in various stages of maturity, and the paraboloid beak. × 190. Fig. 6. Longitudinal section of a perithecium showing numerous paraphyses, immature asci, and ostiolate beak. × 125. FIG. 7. Transverse section of a perithecium showing asci, ascospores, and paraphyses. × 125.

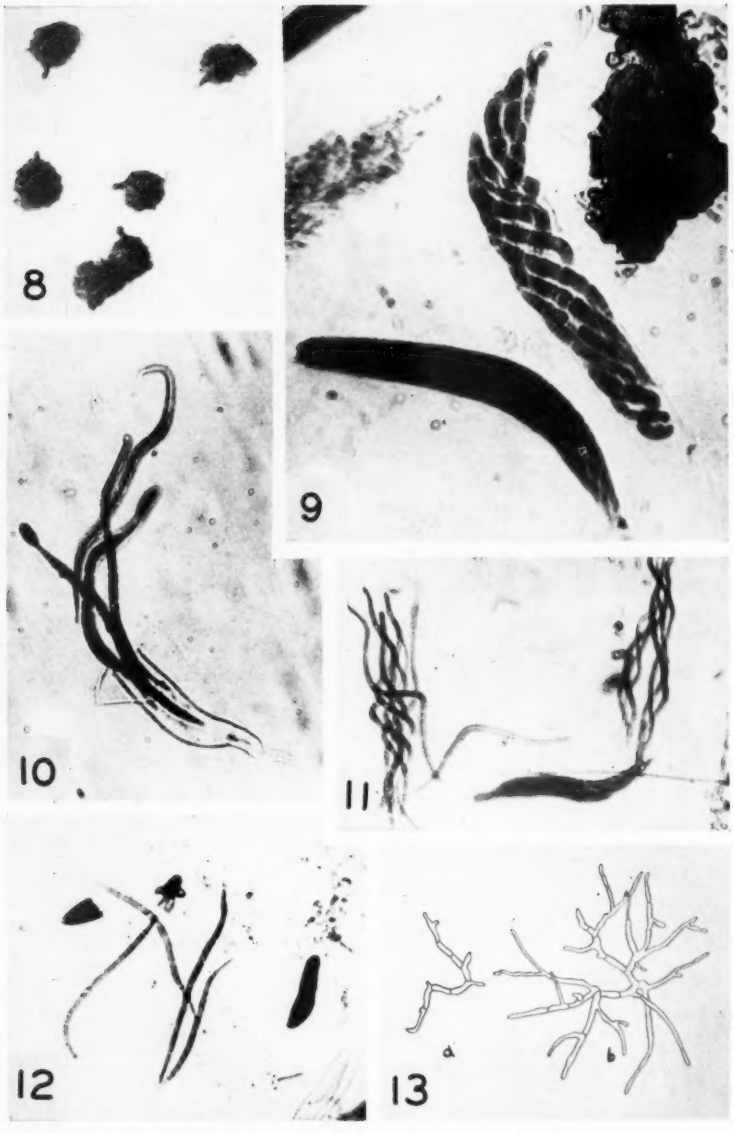

FIG. 8. Beaked perithecia. × 15. FIG. 9. Asci showing helicoid arrangement of the spores. Ascus, upper right, has swollen perceptibly, likely prior to dehiscence. Note distended ascus wall. × 320. FIG. 10. Ascospore escape by a circumscissile rupture of the upper ascus wall. × 210. FIG. 11. Partially uncoiled ascospores after dehiscence. × 150. FIG. 12. Four ascospores and a conidium. × 150. FIG. 13. Germinating ascospore on potato dextrose agar, (*a*) 6 hr., (*b*) 24 hr., after isolation. Camera lucida drawing. × 90.

STUDIES IN FOREST PATHOLOGY

VIII. DECAY OF WESTERN HEMLOCK ON THE QUEEN CHARLOTTE ISLANDS, BRITISH COLUMBIA[1]

By R. E. Foster[2] and A. T. Foster[3]

Abstract

An investigation of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) on the Queen Charlotte Islands, British Columbia, has shown that decay losses in old-growth stands are appreciable, amounting to 13.9, 8.0, and 10.7% of the gross volume of Grades 1, 2, and 3 logs respectively. Total loss, including dead trees, amounted to 25.5% of the gross volume. Twenty-seven decay-producing fungi have been isolated. The most important of these are *Fomes pinicola* (Sw.) Cke., *F. pini* (Thore) Lloyd, *F. annosus* (Fr.) Cke., and *Polyporus sulphureus* Bull. ex Fr. *Echinodontium tinctorium* E. & E. apparently does not occur in the region. Scars provided the most frequent, and roots the most important, avenue of entrance for decay. The logs of 2318 western hemlock were analyzed in detail. Decay was found to increase progressively with diameter, age, and decreasing site quality. Maximum net periodic increment was reached between 350 and 400 years of age and between 35 and 40 in. in diameter. Color of bark was found to provide an added indication of tree maturity. Understory trees were found to give a substantial yield of sound wood.

Introduction

It has been estimated (26) that 75% of the productive forest land on the coast of British Columbia is covered by mature and overmature timber. Stands of this nature may be expected to contain substantial amounts of decay. Accordingly, it is desirable to have information that would assist in evaluating the actual sound wood content of diseased timber and in determining the rate of progressive deterioration. Investigations of the various organisms that cause decay, their frequency of occurrence, points of entrance and relationships to age, diameter, and site are essential requirements in this regard.

To obtain information of this nature for western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) on the Queen Charlotte Islands and to supplement previous information (5) on Sitka spruce (*Picea sitchensis* (Bong.) Carr.), field investigations were conducted by the Dominion Laboratory of Forest Pathology, Victoria, from 1945 to 1947. The present report constitutes a summary and interpretation of information derived from the analysis of 2318 hemlock and 391 spruce which occurred on 47 acres of representative forest land in the region under consideration.

[1] *Manuscript received June 26, 1951.*

Contribution No. 18, Division of Forest Biology, Science Service, Department of Agriculture, Ottawa, Canada. The original manuscript, in part, was submitted by the senior author in partial fulfillment of the requirements for the Degree of Doctor of Philosophy at the University of Toronto, November, 1949.

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Review of Previous Investigations

An examination of the available literature has failed to reveal any comprehensive information relative to the decays and decay relationships of western hemlock on the Queen Charlotte Islands. Various studies pertaining to this species, however, have been undertaken in other forest regions of British Columbia, in adjacent parts of the United States, and in Alaska.

In 1918 Weir and Hubert (27) reported on a study of heart rot in western hemlock in Idaho, a region outside the commercial range of the species. Although some decay was attributed to *Trametes pini* and *Polyporus schweinitzii*, most of the loss was considered to result from the Indian paint fungus, *Echinodontium tinctorium* E. & E. On the basis of this study and from correspondence with timber and mill operators it was concluded that the latter fungus was the cause of practically all of the heart rot in hemlock throughout the Northwest.

The deterioration of wind-thrown hemlock and other coniferous species was considered by Boyce (7) in 1929. Although some initial loss was attributed to ambrosia beetles and stain, extensive breakdown of the heartwood was not evident until the fourth season following death. At the end of five years western hemlock was almost completely deteriorated with 92% of the gross volume destroyed.

In 1932 Eades (12) published a summary of the decays and natural defects of British Columbia softwoods. The important decays of western hemlock considered in this report included *Trametes pini*, *Fomes laricis*, *F. roseus*, *F. annosus*, *Polyporus sulphureus*, *P. abietinus*, *Ganoderma oregonense*, and *Echinodontium tinctorium*.

A further study of the decay and other volume losses in wind-thrown timber on the Olympic Peninsula was presented by Buchanan and Englerth (10) in 1940. The greatest loss from decay was recorded in the case of western hemlock with 93.7 and 100.0% of the board foot volume destroyed at the end of five and eight years respectively. It was concluded that coniferous species should be salvaged within one or two years in order to minimize the losses from decay.

In 1942 Englerth (13) reported on the condition of 801 living trees analyzed within the commercial range of hemlock in Oregon and Washington. Information was provided that would be of assistance to cruisers and scalers in estimating the volume of rot in trees having external indications of decay. Sixteen species of fungi were recorded as causing measurable amounts of decay. *Fomes pini* (Thore) Lloyd was responsible for the greatest number of infections and *F. annosus* (Fr.) Cke. for the greatest loss in volume. *Echinodontium tinctorium* E. & E., formerly regarded as the most serious rot in western hemlock, ranked seventh in order of importance on the basis of the volume of wood destroyed. All infections caused by this fungus were confined

to the Cascade area. It was found that decay was frequent in western hemlock between 60 and 85 years of age, but did not become extensive on the sites studied until trees were approximately 200 years of age.

In the same year Baxter and Varner (2) referred to the occurrence of *Trametes serialis* Fr., *T. alaskana* Baxter, *Poria subacida* Pk., *Fomes nigrolimitatus* Romell, and *Stereum abietinum* Pers. on western hemlock in Alaska. The latter fungus was reported in the vicinity of mill yards and on structural timbers.

A preliminary analysis of the decay losses following logging injury to western hemlock was issued by Englerth and Isaac (15) in 1944. It was found that 90% of the scars resulting from partial cutting had become infected and that an extensive development of decay had taken place during the 16-year period following logging.

In 1945 Bier (3) reported on a preliminary study of decay in the Lower Kitimat region of British Columbia. Based on a sample of 98 hemlock, an average volumetric loss of 26% was recorded in the old-growth stand which contained an understory of trees in varying stages of suppression. Relatively small volumes of decay were recorded in trees less than 250 years of age. Fifty-four per cent of the total decay was attributed to *Trametes pini* (Thore) Fr., 19% to *Echinodontium tinctorium* E. & E., and 9% to *Fomes hartigii* Allesch.

In the same year Foster (16) reported on the decays and decay relationships of western hemlock and amabilis fir in the Franklin River area on Vancouver Island. Based on a sample of 323 western hemlock an average cull factor of 25% was recorded. Approximately 11% of the gross volume was destroyed in trees of the 250-year age class. Thirty-nine per cent of the total decay was attributed to *Fomes pinicola* (Sw.) Cke., 13% to *F. annosus* (Fr.) Cke., 10% to *F. pini* (Thore) Lloyd, 9% to *Armillaria mellea* (Vahl) Quel., and 5% to *Poria subacida* (Pk.) Sacc.

The occurrence of fungi in the major forest types in Alaska was reported by Baxter (1) in 1945. In the coastal area *Fomes pini* (Thore) Karst. and *F. pinicola* Sw. ex Cooke were found to be responsible for the most important decays in western hemlock. On the basis of evidence obtained in the coastal and interior regions it was concluded that environmental factors have a marked influence upon the incidence of forest fungi.

In 1947 Wright, Rhoads, and Isaac (28) issued a further report on the decay losses following logging injury. It was found that *Fomes annosus* was responsible for more than 50% of the decay associated with trunk wounds in western hemlock.

In the same year Englerth (14) reported on the decays of Sitka spruce and ther conifers in Alaska. It was indicated that *Hydnum abietis* appeared too

be one of the most important decays of western hemlock in the southeastern portion of this region.

An interim report on the decays of western hemlock on the Queen Charlotte Islands was prepared by Foster (17) in 1947. On the basis of a sample of 1525 living trees, decay was found to cause a loss of 10.1% in gross volume. A tree classification system for hemlock, based on diameter cutting limits and anticipated sound wood volume, was proposed.

In 1949 Buckland, Foster, and Nordin (11) issued a final report on the decays and decay relationships of western hemlock in the Franklin River area of Vancouver Island. On the basis of a sample of 963 western hemlock it was found that approximately 12% of the gross volume was destroyed in trees of the 250-year age class. Forty-one per cent of the total decay was attributed to *Fomes pinicola* (Sw.) Cke., 13% to *F. pini* (Thore) Lloyd, 10% to *Poria subacida* (Peck) Sacc., 7% to *Fomes annosus* (Fr.) Cke., and 6% to *Armillaria mellea* Vahl ex Fr.

Preliminary information relative to the analysis of 455 western hemlock on Sites 80 and 100 was provided by Foster and Craig (18) in 1950 for the Big Bend region of British Columbia. Extensive decay losses were recorded, reaching 53% in the case of pulpwood utilization in cubic feet and 70% in sawtimber utilization in board feet. Over 60% of the total decay was attributed to *Echinodontium tinctorium* E. & E., 16% to *Fomes pini* (Thore) Lloyd, and 2.5% to *Stereum abietinum* Pers.

In 1950 Browne, Foster, and Thomas (9) reported on the condition of 95 hemlock sampled in the Upper Kitimat region of British Columbia. An average cull factor in board feet of 67% was recorded on Site 100. Approximately 36% of the total decay was attributed to *Fomes pini* (Thore) Lloyd, 19% to *Echinodontium tinctorium* E. & E., and 8% to *Stereum sanguinolentum* A. & S.

From this review of literature it is evident that significant differences on a regional basis are to be anticipated in the complex of decay-producing fungi, and their associated volumes of cull. In view of the apparent lack of information relating to the analysis of factors contributing to excessive variations of the nature mentioned, it is further evident that regional boundaries cannot at present be defined with any degree of accuracy. Accordingly, there appears to be insufficient evidence on hand to permit the direct application of previous findings to the Queen Charlotte Islands region.

Forest Resources of the Queen Charlotte Islands

The total volume of merchantable[4] timber on the Queen Charlotte Islands has been estimated (21, 22) at over 11.5 billion board feet. Ninety-four per

[4] *Trees over 11 in. in diameter at breast height.*

cent of this stand has been classed as accessible and the proportion of the different species by volume was as follows:

Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)	46%
Sitka spruce (*Picea sitchensis* (Bong.) Carr.)	34%
Western red cedar (*Thuja plicata* Donn)	18%
Yellow cedar (*Chamaecyparis nootkatensis* Spach)	2%

It is apparent from the preceding distribution of stand volume that western hemlock is the principal constituent of the stand. Many of the trees are of exceptionally high quality. Sitka spruce, although ranking second in order of abundance, is generally considered to reach its maximum development in these Islands. Most of the trees are of large diameter and good form and contain a high proportion of first grade material. Western red cedar forms approximately 20% and yellow cedar 2% of the stand by volume. Both species contribute to the fact that the Queen Charlotte Islands form a permanent pulp unit in which high grade lumber and special products are also available.

In general, two main forest types are recognized (19). Bier *et al.* (5) describes these as follows:—

"(*a*) *Bench Type*—More open stands of spruce at the lower elevations in valley bottoms and on gentle slopes to creeks, lakes, and salt water. For the most part the areas are well drained. The spruce have a large diameter, but frequently are not so tall as those of the slope type. Typically the stand contains scattered, old-growth spruce, with an understory of western hemlock and spruce.

"(*b*) *Slope Type*—Dense stands of hemlock, spruce, and western red cedar which occur on the steeper side hills. Hemlock appears to be the predominant species. Although the slopes provide excellent drainage the soil retains sufficient moisture to support a good growth of spruce. The trees are taller and less limby than those of the bench type."

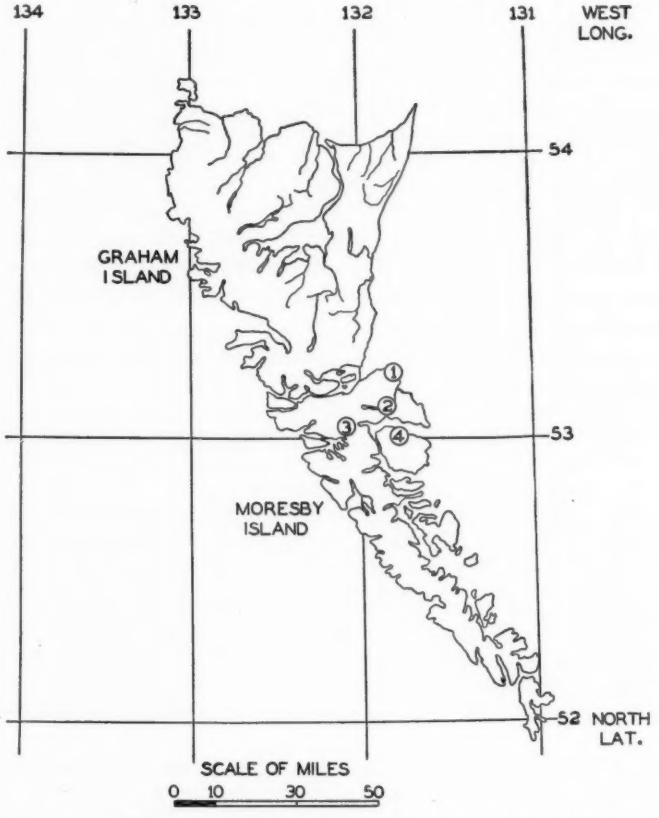
Douglas fir (*Pseudotsuga taxifolia* (Poir.) Britt.), western white pine (*Pinus monticola* Dougl.), and the true firs (*Abies* spp.) do not occur in natural stands in the region under consideration. Shore pine (*Pinus contorta* Dougl.) is found on the northern half of Graham Island and at various other points, but it not widely distributed over the region.

The Queen Charlotte Islands have been established as a Provincial Forest. It is estimated (21, 22) that the accessible stocked areas in the unit have an annual sustained-yield capacity of approximately 187 million board feet. It is evident, therefore, that these Islands constitute a valuable reserve of timber and that western hemlock is a very important component of the stand.

Method of Study

Location of Sample Areas

The field work reported in this study was carried out in the Queen Charlotte Islands, a group situated in the north coastal region of British Columbia, approximately 50 to 90 miles from the mainland (Text-fig. 1).



TEXT-FIG. 1. Map of the Queen Charlotte Islands, B.C. The circles represent the approximate locations of the areas studied, as follows: (1) Sandspit, Big Point, Copper Bay, (2) Skidegate Lake, Cooper River, (3) Mosquito Lake, (4) Louise Island.

Since it was necessary to confine the analysis to areas of active logging, it was not possible to select for study localities representative of the entire range of conditions in which hemlock is known to occur in these Islands. During the three years of the study, for example, it was possible to locate only one, Site 80, area in which felled trees were available for analysis. Most of the cutting was confined to Sites 100 and 120. Similar problems were encountered in the case of average stand age, forest type, slope, and elevation. At the same time, however, extensive variations in these several factors were not anticipated, owing to the generally uniform conditions believed to prevail over most of the region.

Ten areas were examined during the course of the study. Basic information pertaining to these is presented in Table I.

It is to be noted that the average stand age of hemlock of merchantable size[5] varied from 220 years at Sandspit to 368 years at Skidegate Lake. Subsequent analyses in the latter area provided further evidence of overmaturity, individual hemlock in excess of 700 years and cedar over 1000 years of age being found. The Site 120 area at Skidegate Lake was characterized by an exceptionally heavy concentration of hemlock. By volume, the stand composition in this area was approximately 85% hemlock, 7% spruce, and 8% red cedar. A dense understory of hemlock occurred throughout the latter area. The lightest concentrations of hemlock, 27 to 29%, were obtained at Sandspit and on Louise Island. In the remaining areas the stands contained from 46 to 70% hemlock by volume.

The areas examined were considered to be representative of the range in forest type, slope, and elevation in which hemlock is known to occur in commercial stands on the Queen Charlotte Islands. The Copper River and Louise Island samples were situated on poorly drained bottomland sites at elevations above sea level of from 50 to 100 ft. The 4-acre sample at Skidegate Lake was situated on a lower bench site at an elevation of between 25 and 250 ft. above sea level. The 8.2-acre sample at Skidegate Lake was located for the most part on an upper bench at an elevation of 1000 ft. above sea level and in part on an adjacent 17% southern slope. The Site 120 samples at Skidegate Lake and Copper Bay were situated on 25 and 30% western and eastern exposures respectively. Plots in the former area were located at an elevation of approximately 800 ft. and in the latter at approximately 100 ft. above sea level.

Decay, expressed in relation to the gross merchantable volume per acre, varied from 15.1 to 45.1%.

Field Procedure

Sample plots were established in all areas of felled and bucked timber containing a sufficient concentration of hemlock to warrant analysis. The size of the plots varied with local conditions, such as topography, width of

[5] *Fifteen inches and over in diameter at breast height in the case of western hemlock and Sitka spruce, and 20 in. and over in diameter in the case of western red cedar.*

TABLE I

BASIC DATA PERTAINING TO SAMPLE AREAS OF WESTERN HEMLOCK ON THE QUEEN CHARLOTTE ISLANDS

Locality	Area (acres)	Hemlock of merchantable size						Gross volume per acre percentage of stand		
		Site	Number	Average d.b.h. (in.)	Average age (years)	Gross volume per acre (f.b.m.)	Percentage of decay	Hemlock	Spruce	Cedar
Sandspit	2.00	100	66	28.3	271	39,970	17.4	29.1	70.9	—
Sandspit	5.00	100	215	26.2	220	39,040	21.0	48.3	51.7	—
Big Point	9.00	120	464	28.7	260	72,460	18.4	50.6	49.4	—
Copper Bay	1.25	120	51	27.6	347	41,240	24.1	46.5	48.1	5.4
Copper River	3.20	120	223	27.5	288	68,430	35.8	58.6	35.2	6.2
Skidegate Lake	8.20	100	379	34.2	368	78,360	45.1	76.3	14.3	9.4
Skidegate Lake	4.35	120	251	28.3	274	81,640	15.4	85.5	6.9	7.6
Skidegate Lake	4.00	100	235	27.0	272	63,900	15.1	70.5	28.6	0.9
Mosquito Lake	7.00	120	300	29.7	302	64,940	19.4	46.7	53.0	0.3
Louise Island	3.00	80	134	25.5	264	30,060	29.9	26.9	69.7	3.4
Total or average	47.00	110	2318	28.9	287	63,740	25.5	55.7	41.4	2.9

cutting strip, and location of roads. As far as possible, however, plots of uniform size were used in each locality. Of the 183 plots established, 51 were 0.20 acres in size, 125 were 0.25 acres, and 7 ranged from 0.32 to 2.00 acres. The total area laid out in plots amounted to 47.0 acres.

Pertinent data on all trees were recorded on Tree Measurement Form SSB 228.

All hemlock of merchantable size were scaled[6] from the point at which they were cut to a standard 10-in. top diameter inside bark. The volume contained between these limits was considered to represent the gross merchantable volume according to current standards of utilization. Stump volumes and volumes of logs less than 10 in. top diameter were not computed. In most cases sample areas on which cull and other trees had been left standing were recut in order to provide complete information on a stand basis. A record was kept of the size and condition of the trees forming the understory.[7] Stump diameters and d.b.h.[8] measurements were recorded for the Sitka spruce and western red cedar located within the sample areas.

Individual logs were graded and culled according to the Tables of Grades for western hemlock (25) as follows:

"No. 1—Logs 16 feet and over in length, 26 inches and over in diameter, that will cut out 50 per centum or over of their scaled contents in No. 2 clear, B, or better grade of lumber, and that are free from spiral grain or twist to the extent of a variation of not more than 1 inch per lineal foot for logs 35 inches in diameter and under, and not more than 1½ inches per lineal foot for logs 36 inches in diameter and over the entire length of the log.

"No. 2—Logs not less than 20 inches in diameter and not less than 16 feet in length that will cut out 65 per centum or over of their scaled contents in merchantable or better grade of lumber or 20 per centum or better of a clear grade of lumber with only slight spiral grain or twist in logs 20 inches to 25 inches in diameter, logs 26 inches to 35 inches in diameter, not over 1 inch per lineal foot, and logs 36 inches in diameter and over, not over 1½ inches per lineal foot for the entire length of the log.

"No. 3—Logs lower in grade than No. 2, suitable for the manufacture of pulp and lumber.

"Logs containing less than 50 per centum of their gross scale in sound wood content shall be graded No. 3.

"Culls—Logs containing less than one-third of their gross scale in sound wood content shall be classed as culls."

Volumes were computed in board feet and in cubic feet on the basis of log lengths resulting from actual bucking practice. Short pieces and tops were scaled if the top diameters were 10 in. or greater and were considered

[6] *The scaling was done by a licensed scaler in accordance with the volume and standard scaling practice outlined in the British Columbia Log Scale (24) and Scaling Lessons (23) respectively.*

[7] *Understory trees defined as trees 6-14 in. in diameter at breast height in the case of western hemlock and Sitka spruce, and 6-19 in. in diameter in the case of western red cedar.*

[8] *Diameter at breast height outside bark.*

merchantable if 24 ft. or over in length. The net volumes contained in logs less than 24 ft. long were included under utilization loss[9]. Board foot volumes were based on the British Columbia Log Scale (24) and cubic foot volumes were computed by Smalian's formula.[10]

Deductions in volume for decay were computed by means of accurate diameter measurements and estimates of the lineal extent of rot based on external indications. In some cases logs were bucked into shorter lengths in order to obtain an accurate estimate of the longitudinal extent of the decay column. In most cases, however, the size and value of the timber made this procedure impractical. In the case of heart rot deductions the average diameter of decay was increased by one inch, and the volume of a log having this increased diameter and a length equivalent to two-thirds of the estimated longitudinal extent of the decay column was considered to represent the loss in volume from decay. Sap rot deductions were made by reducing the diameter of the log according to the average extent of penetration of the decay.

Similar culling standards were employed both in board and cubic foot calculations. Cubic foot values are not intended to relate to total sound wood recovery, but rather to the net merchantable volume, derived as a result of arbitrary culling standards similar to those employed in board feet. Thus, only slight differences between the percentage of defect in board and cubic feet are to be anticipated.

A measurement was made of the average stump height of each tree. Data on an age–height relationship for hemlock seedlings were obtained in the vicinity of Sandspit. These data were related to stump ages to provide an estimate of total age. In cases where it was not possible to obtain an accurate or complete age count, the age of the tree in question was considered to be equal to that of adjacent trees of the same diameter and growth characteristics.

Basic Data

A preliminary review of the basic data pertaining to all coniferous species is presented in Table II.

It is apparent from Table II that the stand composition, as measured in number of stems, was predominantly hemlock. It is further evident that areas similar to those examined may be expected to contain relatively high proportions of hemlock in the future, since 3081, or 97%, of the 3159 understory trees were of this species.

Although the average age did not exceed 355 years in any species, the maximum ages were indicative of advanced overmaturity. Thus, individual spruce of 560 years, hemlock of 718 years, and cedar in excess of 1000 years

[9] *The volumes contained in logs less than 24 ft. long after lineal deductions for breakage and volumetric deductions for decay.*

[10] $V = \frac{B + b}{2} \times L$ *where* V = *volume in cu. ft.,* B = *basal area of the large end of the log in sq. ft.,* b = *the basal area of the small end of the log in sq. ft., and* L = *length of the log.*

TABLE II

BASIC DATA FOR ALL CONIFEROUS SPECIES SAMPLED ON THE QUEEN CHARLOTTE ISLANDS

(Basis 47.0 acres)

	Western hemlock	Sitka spruce	Western red cedar	All coniferous species
Understory trees				
Number	3081	53	25	3159
Percentage of total	97.5	1.7	0.8	100.0
Trees of merchantable size				
Number of living trees	2041	351	68	2460
Number of dead trees	277	40	8	325
Total number of trees	2318	391	76	2785
D.b.h. (in.)				
Minimum	15	15	19	15
Maximum	68	114	95	68
Average	29	49	40	32
Age (years)				
Minimum	77	65	124	65
Maximum	718	560	1000	1000
Average	287	341	355	296
Gross volume (M.B.M.)*	2996	2227	157	5380
Percentage of decay	25.5	24.0	38.0	25.2

* *Thousand board feet board measure, British Columbia scale.*

were recorded. A similar situation was found to exist in the case of diameter. Maximum diameters of 68, 95, and 114 in. were recorded for hemlock, cedar, and spruce respectively.

The relative incidence of dead trees varied from approximately 10% in spruce and cedar to 12% in hemlock. A total of 325 dead trees was recorded and their actual or estimated scaled contents included in the gross merchantable volume per acre. The latter decay volume together with the volume of rot in the living trees of the stand necessitated a 25% reduction in the indicated gross volume of 5,380,000 f.b.m.[11]. Sitka spruce was found to be the least defective species with 24% loss from decay, and western red cedar the most defective with 38% loss. Western hemlock occupied an intermediate position with 26% loss from evident and hidden defect. Allowance for further reduction in the case of felling breakage, yarding losses, and hidden defect other than rot would be required to provide an estimate of the average net merchantable recovery per acre. Reliable estimates of the latter nature were considered to be beyond the scope of the present study. Observations indicated, however, that substantial reductions would be required in most cases.

[11] *Foot board measure, British Columbia scale.*

Basic Loss in Western Hemlock

Basic loss data for western hemlock have been summarized in Table III.

TABLE III

BASIC LOSS IN WESTERN HEMLOCK ON THE QUEEN CHARLOTTE ISLANDS

Loss in:	Type of loss	Volume, f.b.m.	Percentage of class total
Dead trees (277 trees) (499,639 f.b.m.)	Decay	499,639	100.0
Living trees (2041 trees) (2,496,323 f.b.m.)	Decay	264,370	10.6
	Falling breakage and utilization	156,689	6.3
	Total loss	421,059	16.9
All trees (2318 trees) (2,995,962 f.b.m.)	Decay	764,009	25.5
	Falling breakage and utilization	156,689	5.2
	Total loss	920,698	30.7

It is to be noted that 277, or 11.9%, of the 2318 trees were dead. Trees in this class contained approximately 500,000 f.b.m., or 16.7% of the total volume. Dead trees were found to contain less than 20% of their volume in sound wood. Accordingly, their entire volume was considered unmerchantable.

In the living trees, falling breakage and utilization losses amounted to approximately 157,000 f.b.m., or 6.3% of the total volume. An additional 10.6% loss was attributed to decay.

On a total stand basis, 25.5% loss was attributed to decay and 5.2% loss to breakage and utilization. Total stand loss from these various factors amounted to 30.7%.

It is evident that over half of the total loss and over 65% of the gross decay may be estimated in standing timber by an analysis of the number and volume of dead trees. Information pertaining to the frequency of occurrence of dead trees would also contribute to a more reliable appreciation of logging costs, since felling and yarding difficulties may be increased considerably through the occurrence of this class of material. In addition, evident cull trees provide an indirect measure of stand maturity. It would appear to be of value in timber estimating, therefore, to record pertinent information on evident culls as well as on trees expected to contain a net merchantable volume.

The information presented in Table III pertains to the average losses to be anticipated in stands of mature and overmature western hemlock on the Queen Charlotte Islands. The data indicate the need for basic information that would contribute to an accurate inventory, a greater utilization, and a sound basis for priority cutting schedules in forest management. In view of

the recorded incidence and importance of the losses attributed to rot, data pertaining to the effect and nature of the various decays and decay relationships are an essential requirement in this regard.

The Decay Fungi of Western Hemlock

Occurrence of Fungi Causing Decay

Although a considerable number of fungi were found in association with decay in living trees, relatively few were of frequent occurrence (Table IV).

TABLE IV

OCCURRENCE OF FUNGI CAUSING DECAY IN LIVING WESTERN HEMLOCK ON THE QUEEN CHARLOTTE ISLANDS

Organism	Number of infections*	Percentage of total infections
Brown rots		
Fomes pinicola (Sw.) Cke.	134	12.1
Stereum abietinum Pers.	91	8.2
Polyporus sulphureus Bull. ex Fr.	63	5.7
Polyporus schweinitzii Fr.	10	0.9
Polyporus fibrillosus Karst.	8	0.7
Fomes laricis (Jacq.) Murr.	5	0.4
Omphalia campanella Fr.	2	0.2
Poria monticola Murr.	2	0.2
Pholiota adiposa Fr.	1	0.1
Total	316	28.5
White rots		
Poria subacida (Pk.) Sacc.	119	10.7
Fomes annosus (Fr.) Cke.	115	10.3
Armillaria mellea Vahl ex Fr.	76	6.8
Fomes pini (Thore) Lloyd	70	6.3
Poria tsugina (Murr.) Sacc. & Trott.	52	4.7
Fomes applanatus (Pers.) Wallr.	35	3.1
Ganoderma oregonense Murr.	30	2.7
Hericium sp.	29	2.6
Polyporus abietinus Dicks. ex Fr.	13	1.2
Polyporus tomentosus Fr.	8	0.8
Stereum sanguinolentum A. & S. ex Fr.	4	0.4
Polyporus volvatus Pk.	4	0.4
Poria decolorans (Schw.) Cke.	3	0.3
Poria nigrescens Bres.	2	0.2
Polyporus montanus (Quél.) Ferry	1	0.1
Polyporus tomentosus var. *circinatus* Fr.	1	0.1
Fomes nigrolimitatus (Rom.) Egel.	1	0.1
Total	563	50.7
Mixed rots	109	9.8
Unknown rots	122	11.0
Total	1110	100.0

* *No attempt has been made to separate multiple infections of the same fungus within individual trees.*

In the latter group, moreover, *Fomes pinicola* (Sw.) Cke., *Poria subacida* (Pk.) Sacc., and *Fomes annosus* (Fr.) Cke. were the only species having an infection rating greater than 10%. *Fomes pinicola*, the fungus of most frequent occurrence, caused only 12% of the total infections.

The occurrence of *Stereum abietinum* Pers. is of interest since this fungus has only recently been reported as a cause of heart rot in living trees (2, 16). The present recorded distribution of the fungus (9, 11, 16, 18) indicates that it may be ubiquitous within the range of western hemlock, at least in British Columbia.

Fomes pini (Thore) Lloyd ranked only sixth in order of frequency of occurrence. This finding is of interest in view of the high incidence of infection by this species in Sitka spruce on the Queen Charlotte Islands (5) and in western hemlock in the coastal region of the neighboring mainland (3, 9).

A species of *Hericium* was isolated from 29 rot samples. Subsequent review of the literature indicated that this was the same organism referred to by Englerth (13) as *Hydnum abietis*, and reported as the cause of a decay of considerable significance throughout the Pacific Northwest, including British Columbia and Alaska (14, 20).

Echinodontium tinctorium E. & E. was not observed on western hemlock on the Queen Charlotte Islands during the course of the study. It is known to occur and to be responsible for appreciable loss, however, on the coastal mainland (3, 9).

Eleven per cent of the infections were listed as unknown. It is possible that further analyses may indicate a relationship with certain of the following fungi which occurred on western hemlock slash on the Queen Charlotte Islands:—

Aleurodiscus pencillatus Burt
Hymenochaete tabacina Sow. ex Lev.
Lenzites saepiaria Wulf. ex. Fr.
Pleurotus petaloides (Fr.) Quél.
Polyporus dryadeus Pers. ex. Fr.
Polyporus guttulatus Pk.
Polyporus picipes Fr.
Polyporus resinosus Schrad. ex. Fr.
Poria ferrea (Pers.) Bourd. & Galz.
Poria subincarnata (Pk.) Murr.
Poria undata (Pers.) Bres.
Poria versipora (Pers.) Rom.
Stereum chailletii Pers.
Trametes serialis Fr.
Trechispora brinkmanni (Bres.) Rogers & Jacks.
Vararia granulosa (Pers. ex Fr.) Laurila

In order of descending importance the most common fungi in evident cull trees were *Fomes pinicola*, *F. applanatus* (Pers.) Wallr., *Ganoderma oregonense* Murr., and *Fomes annosus*. These species caused over 75% of the total infections in this class of material.

Avenues of Entrance of Infection

On the basis of field observations and analyses, five points of entrance for wood-destroying fungi were recognized during the course of the study (Table V). Falling-tree, fire, lightning, and frost scars were found to cause a total of 31% of the infections. Most of the injuries, however, resulted from falling

TABLE V

INFECTION COURTS OF THE PRINCIPAL FUNGI ASSOCIATED WITH THE DECAY OF WESTERN HEMLOCK ON THE QUEEN CHARLOTTE ISLANDS

Fungus	Percentage of total number of infections				
	Scars	Roots	Branches and branch stubs	Dead tops	Mistletoe knots and burls
Root and butt rots*					
Poria subacida	13	87			
Fomes annosus	30	70			
Armillaria mellea	24	76			
Polyporus sulphureus	56	44			
Hericium sp.	44	56			
Polyporus schweinitzii	—	100			
Others	27	73			
Mixed	32	68			
Unknown	37	63			
Total	28	72			
Trunk rots*					
Fomes pinicola	33	—	36	16	15
Stereum abietinum	24	—	67	9	—
Fomes pini	11	—	85	4	—
Poria tsugina	15	—	25	27	33
Fomes applanatus	60	—	17	6	17
Ganoderma oregonense	47	—	20	6	27
Polyporus sulphureus	38	—	21	33	8
Others	41	—	45	14	—
Mixed	47	—	44	5	4
Unknown	50	—	30	19	1
Total	34	—	43	14	9
Total all decay	31	30	26	8	5

* *As determined by the location of the associated decay.*

trees and these were considered to have greater significance in regard to decay, owing to the generally extensive area exposed to infection. The susceptibility of western hemlock to scar damage may be related in part to the relatively

thin bark and in part to the absence of a copious supply of resin. The resulting losses from decay constitute an important factor in the management of this species.

Root infections, although ranking second in order of the total number of infections, were of primary importance owing to the initiation of decay in the lower part of the tree. In addition, butt and root infections were found to contribute to mortality losses in all age classes, following a weakening or partial destruction of the root system with subsequent windfall.

Dead and broken branches served as an important avenue of entrance in most age classes. Branches hypertrophied by mistletoe were grouped separately under "mistletoe knots and burls". The actual number of branch infections, therefore, was considerably greater than has been indicated.

The tops of a considerable number of western hemlock were found to be either dead or in a very weakened condition. Insects, lightning, wind, mistletoe, fungi, and general overmaturity were considered to be contributing factors to this condition.

An appreciable number of infections were found in association with the dwarf mistletoe (*Arceuthobium campylopodum* forma *tsugensis* (Rosendahl) Gill). This plant is a parasite of considerable importance. In addition to providing entrance courts for wood-destroying fungi, mistletoe may reduce the rate of growth and vitality of the host, and severe infections may kill mature trees or deform them to the extent that they become of doubtful value for the production of lumber. The appearance of dwarf mistletoe and its effect on western hemlock is shown in Plate I.

Relative Importance of the Principal Decays

Quantitative Losses

It has been shown (Table III) that 10.6% of the gross volume in residual trees was affected by decay. Further information pertaining to the relative losses associated with the more important decay-producing fungi is presented in Table VI. It can be seen (Column 9) that the loss in volume caused by *Fomes pinicola* exceeded that caused by any other fungus, with 1.6% of the gross volume destroyed. Next in order of importance were *F. pini* with 1.4%, *F. annosus* with 1.2%, and *Polyporus sulphureus* Bull. ex. Fr. with 1.0%. Each of the remaining fungi accounted for a loss of less than 1.0% of the gross volume.

In the case of evident cull trees approximately 65% of the volume was destroyed by *Fomes pinicola*, 12% by *F. applanatus*, 7% by *F. annosus*, and 4% by *Ganoderma oregonense*. Nine additional fungi were recorded in association with the deterioration of this class of material.

Qualitative Losses

In western hemlock and other coniferous species, it may be misleading to state the loss from decay only as a percentage of the gross volume. Since the grade of logs is important, percentage of loss on a volume basis does not

TABLE VI

RELATIVE IMPORTANCE OF THE PRINCIPAL DECAYS OF WESTERN HEMLOCK ON THE QUEEN CHARLOTTE ISLANDS

(Basis 2041 living trees)

Organism	Grade 1 logs total volume, 587,257 f.b.m.		Grade 2 logs total volume, 822,850 f.b.m.		Grade 3 logs total volume, 1,086,216 f.b.m.		All logs total volume, 2,496,323 f.b.m.	
	Decay volume, f.b.m.	Percentage of total volume, Grade 1	Decay volume, f.b.m.	Percentage of total volume, Grade 2	Decay volume, f.b.m.	Percentage of total volume, Grade 3	Decay volume, f.b.m.	Percentage of total volume, all logs
Brown rots								
Fomes pinicola	4201	0.7	10,952	1.3	23,656	2.2	38,809	1.6
Polyporus sulphureus	14,758	2.5	3893	0.5	6292	0.6	24,943	1.0
Stereum abietinum	1241	0.2	3011	0.4	10,125	0.9	14,377	0.6
Polyporus schweinitzii	826	0.2	2590	0.3	—	0.3	3416	0.1
Other brown rots	87	—	276	—	1752	0.1	2115	0.1
Total	21,113	3.6	20,722	2.5	41,825	3.8	83,660	3.4
White rots								
Fomes pini	3550	0.6	8534	1.0	22,043	2.0	34,127	1.4
Fomes annosus	18,049	3.1	5787	0.7	5942	0.6	29,778	1.2
Armillaria mellea	12,868	2.2	3570	0.4	2500	0.2	18,938	0.8
Poria subacida	7098	1.2	4023	0.5	1510	0.2	12,631	0.5
Poria tsugina	531	0.1	2246	0.3	7711	0.7	10,488	0.4
Fomes applanatus	1894	0.3	2905	0.4	3581	0.3	8380	0.3
Hericium sp.	3257	0.6	2756	0.3	1159	0.1	7172	0.3
Ganoderma oregonense	105	—	1599	0.2	4580	0.4	6284	0.2
Polyporus abietinus	6	—	595	0.1	2098	0.2	2699	0.1
Other white rots	2533	0.5	994	0.1	1525	0.1	5052	0.2
Total	49,891	8.5	33,009	4.0	52,649	4.8	135.549	5.4
Mixed	1921	0.3	5306	0.6	10,334	1.0	17,561	0.7
Unknown rots	8869	1.5	7236	0.9	11,495	1.1	27,600	1.1
Total decay	81,794	13.9	66,273	8.0	116,303	10.7	264,370	10.6

necessarily coincide with loss in quality. Accordingly, the method first introduced by Bier *et al.* (5) has been used to indicate comparative losses on the basis of value.

On the Basis of Grade 1 Logs.—The total volume of Grade 1 logs amounted to 587,257 f.b.m., or 23.5% of the gross volume. Approximately 14% of this volume was destroyed by decay. *Fomes annosus* was responsible for the greatest loss in Grade 1 material, with 3.1% of the volume destroyed. Second in importance was *Polyporus sulphureus* with 2.5% loss. In previous studies (5, 8, 13) this fungus has generally been assigned a relatively unimportant position as a trunk rot. From the present study it is evident that this view is not tenable for western hemlock on the Queen Charlotte Islands. It has been noted (Table V) that roots provided a common point of entrance for this species and it is considered that basal infections of this nature were largely responsible for the high percentage of loss in Grade 1 logs. Forty-six per cent of the infections caused by *P. sulphureus* gained entrance through various types of scars. A further analysis of the basic data has shown that over half of these occurred in Grade 1 logs. *Armillaria mellea* Vahl ex Fr. and *Poria subacida* were also responsible for considerable loss in volume in this class of material. *Fomes pinicola* and *F. pini*, however, were of relatively minor importance, causing only 0.7 and 0.6% loss respectively.

On the Basis of Grade 2 Logs.—The total volume of Grade 2 logs amounted to 822,850 f.b.m., or 33% of the gross volume. Decay was responsible for a loss of 8%. *Fomes pinicola* and *F. pini* were the only organisms responsible for 1.0% or greater loss. Thirteen other species, however, were isolated from this grade of material. Since Grade 2 logs are required to cut out only 20% or better of a clear grade of lumber, the more frequent occurrence of fungi associated with branch infections is to be anticipated.

On the Basis of Grade 3 Logs.—The gross volume of Grade 3 logs measured 1,086,216 f.b.m., or 43.5% of the total volume scaled. The volume of decay in Grade 3 logs amounted to 116,303 f.b.m., or 10.7% of the total volume of this grade. As in the case of Grade 2 material, *Fomes pinicola* and *F. pini* were the only two fungi of major importance, causing 2.2 and 2.0% loss respectively. Several of the lesser decays, however, caused greater loss in volume in Grade 3 than in either Grade 1 or Grade 2 material. The latter condition was found to be true in the case of *Stereum abietinum*, *Poria tsugina* (Murr.) Sacc. & Trott., and *Ganoderma oregonense*. Several of the fungi associated with root and butt rots contributed to a loss in Grade 3 logs. Among these were *Fomes annosus*, *Armillaria mellea*, and *Poria subacida*. It does not necessarily follow, however, that these species were associated with trunk decay in the upper part of the tree. As a matter of record, it should be noted that all of the latter infections were confined to the basal portion of the tree. Because of the diameter requirements for Grade 1 and Grade 2 logs, many basal logs in trees 25 in. or less were placed in Grade 3.

The quality requirements of the better grades necessitated the degrading in a number of other cases of logs meeting the specifications of Grades 1 or 2 on the basis of size alone.

The occurrence of decay-producing fungi on the Queen Charlotte Islands appears to confirm in large part previous analysis of western hemlock in the southern coastal region (11, 16). The findings do not agree, however, with studies undertaken in the region east of the Cascade Range[12] (18, 27) or in other regions in the northern coastal area (3, 9). In the latter localities *Echinodontium tinctorium* and *Fomes pini* have previously been recorded as the commonest and most important fungi associated with the decay of western hemlock. In the present study, however, neither the incidence nor the importance of *F. pini* warranted any particular concern, despite its high frequency of occurrence in Sitka spruce in the same area. *Echinodontium tinctorium*, moreover, is as yet unreported in the Queen Charlotte Islands. This study did not provide any evidence of the abnormal incidence or outstanding importance of any single species on living hemlock. The most common fungus, *Fomes pinicola*, was responsible for only 15% of the total decay. On the nearby mainland, however, Bier (3) has assigned 54% and Browne (9) 36% of the total decay to this species. In both cases, moreover, 19% of the total decay was assigned to *Echinodontium tinctorium*. It may be concluded that the present data support previous evidence of the regional variation to be anticipated in the complex of decay-producing fungi. It is further evident that the present findings emphasize the need for more intensive studies relative to the designation of regional boundaries and the analysis of factors contributing to decay.

External Indications

In many cases information that would confirm the presence or absence of heart rot and provide a reliable estimate of the amount of hidden defect in individual trees would be of considerable practical value. Initially, it would be necessary in this connection to evaluate the significance of all known or assumed indicators of internal defect, such as exposed roots, open scars, dead branches, swollen knots, broken tops, and sporophores. In order that the derived correlations could be applied in forest inventory and related practices, it would be equally essential that the analyses be restricted to features evident in standing timber. The present study was confined to felled and bucked timber and it was not possible to undertake correlation analyses on a sufficiently extensive or reliable basis to provide information of the nature required. Enough evidence was obtained, however, to indicate that analyses restricted to the interpretation of sporophores would provide only a partial solution to the problem. Thus, many of the organisms associated with the heartwood deterioration of living western hemlock produced abundant sporophores on standing snags, slash, and other dead material on the ground,

[12] *Commonly referred to as the Interior Region or Interior.*

but seldom, if ever, produced fruiting bodies on living trees. This was particularly evident in the case of *Fomes pinicola*, *F. annosus*, *F. applanatus*, *Poria subacida*, and *Ganoderma oregonense*.

In several cases, even where the fruit bodies were produced on living trees, their size and location rendered their presence of limited practical value. The size and coloration of *Stereum abietinum*, the frequent occurrence of *S. sanguinolentum* A. & S. ex Fr. in the upper crown, and the camouflaged nature of *Poria tsugina* are illustrative of the inherent difficulties. *Fomes pini* provided the most consistent and reliable evidence. Even in this case, however, sporophores were recorded on only 21 of the 70 trees known to be infected.

Therefore, although certain sporophores may provide reliable external indications of the presence of defect in living trees, most heart rot must be classed as hidden defect.

Descriptions of the Principal Decays

The principal decays associated with western hemlock on the Queen Charlotte Islands were not found to vary to any appreciable extent from those recorded in other nearby regions (4, 11). Accordingly, only brief descriptions are included in the present report (Plates II-VI). Additional information obtained in the case of *Stereum abietinum*, *Poria nigrescens* Bres., and *Hericium* sp. (*"Hydnum abietis"*), however, makes it possible to supplement previous records.

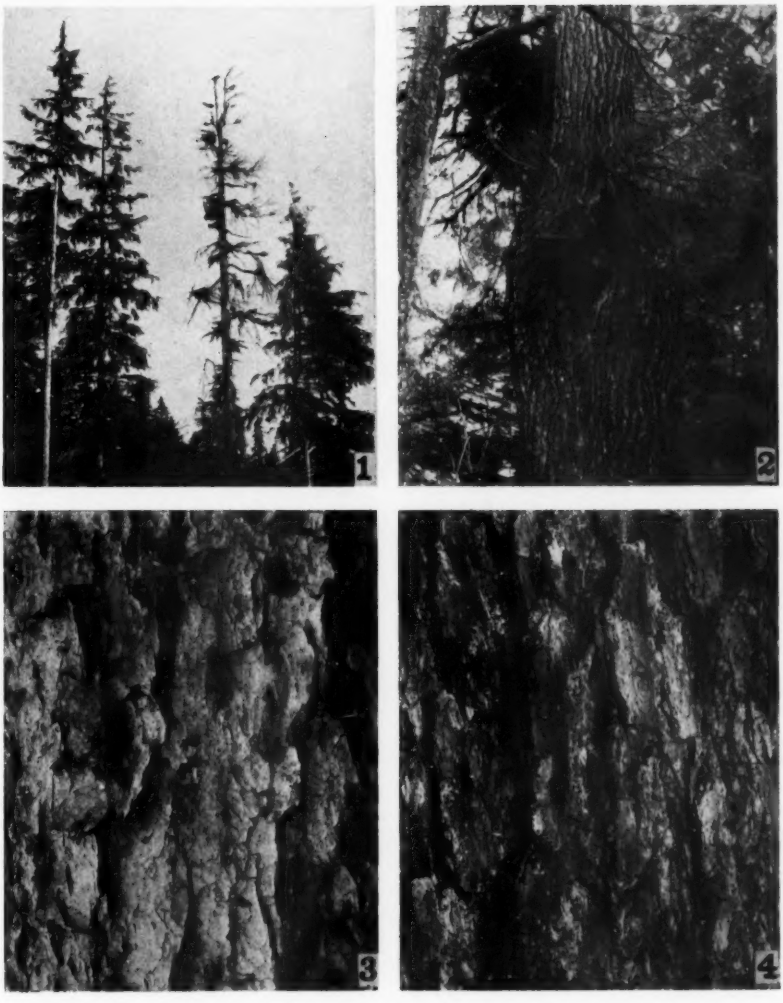
Brown Cubical Pocket Rot Caused by Stereum abietinum

In the early stage of decay the infected portions are characterized by a light brown stain. Later, the wood is reduced to brown cubical formations which are often confined to isolated pockets and surrounded by what appears to be sound wood. Adjacent pockets may coalesce to form more or less continuous areas of decay. The cubes are light to dark brown in color, soft, and easily pulverized. Mycelial tufts or thin felts, white to cream in color, may form in the shrinkage cracks, but these are seldom if ever extensive. Fresh samples of the decay have a characteristic odor that becomes more evident when the sample is moistened. A similar odor occurs in pure strain cultures of the fungus, indicating that the substance or substances responsible are produced independently of the host tissues. A black streak or stain may generally be found adjacent to advanced stages of the decay (Plate VI).

Brown Fibrous Rot Caused by Poria nigrescens

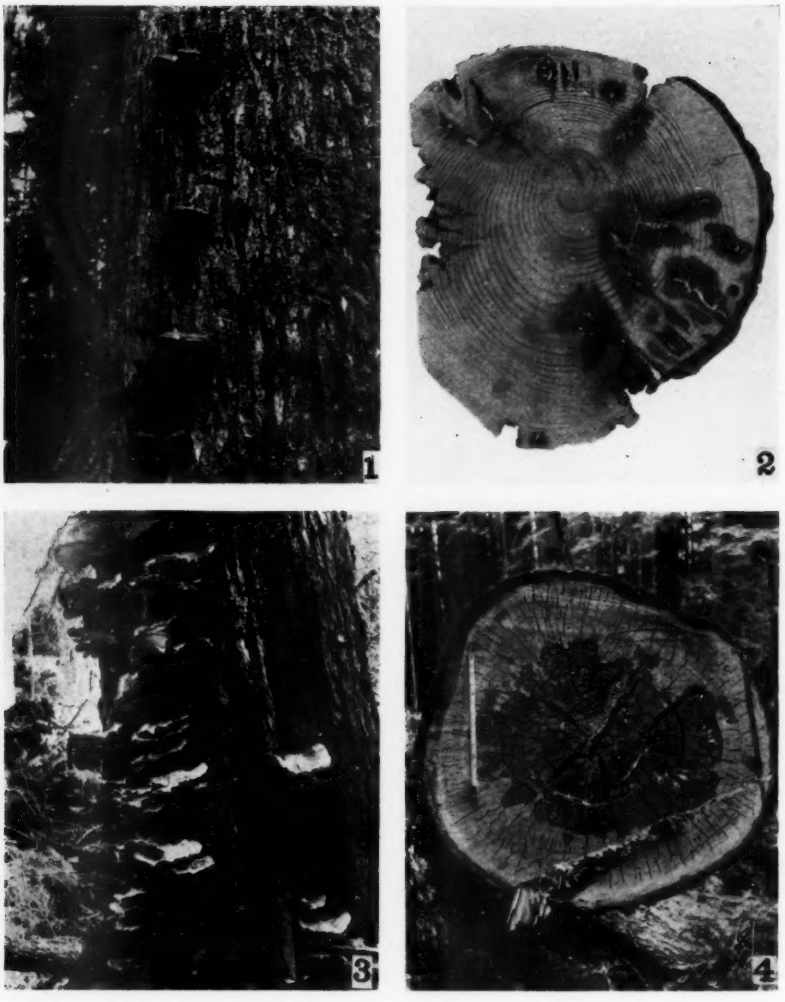
The incipient stage is marked by a pink to light brown discoloration. Small, white to light yellow pits appear at an early stage. The pitted nature of the decay may be obscured, however, by a brown mottling effect and lamination. Later, the pits coalesce to form a light brown, stringy heart rot, soft and fibrous in texture. Complete destruction of the heartwood is

PLATE I



Arceuthobium campylopodum f. *tsugensis* and bark types in western hemlock.

FIG. 1. A mature tree killed by dwarf mistletoe.
FIG. 2. Old mistletoe infection providing an avenue of entrance for *Fomes pinicola*.
FIG. 3. Light bark of western hemlock showing the thin, scaly texture.
FIG. 4. Dark bark of western hemlock showing the thick, ridged texture.



Fomes pinicola and *Polyporus sulphureus* in living western hemlock.

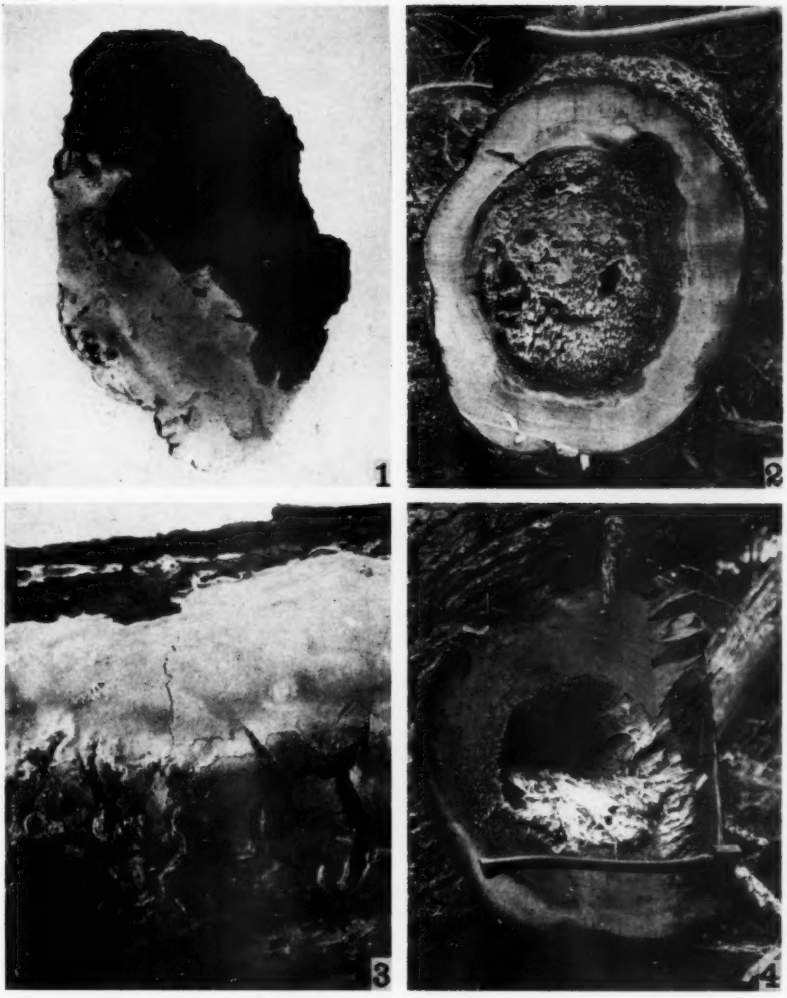
FIG. 1. Sporophores of *Fomes pinicola* at the base of western hemlock serving as an indication of extensive decay.

FIG. 2. Cross section of a decayed stem showing the cubical nature of the decay and the occurrence of white mycelial felts of *Fomes pinicola*.

FIG. 3. Fruiting bodies of *Polyporus sulphureus* at the base of western hemlock serving as an indication of extensive decay.

FIG. 4. Decay caused by *P. sulphureus*.

PLATE III



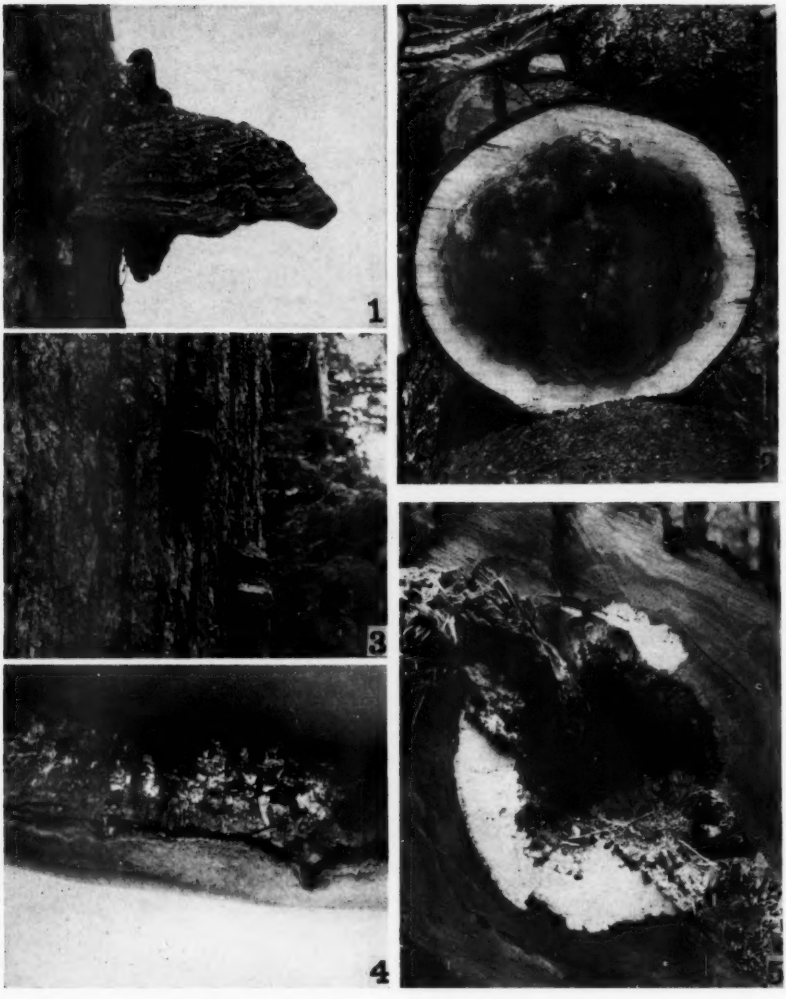
Fomes annosus and *Poria subacida* in living western hemlock.

FIG. 1. Sporophore of *Fomes annosus* on an infected root.

FIG. 2. The appearance of the decay caused by *F. annosus* showing the white spongy nature of the rot.

FIG. 3. Fruiting body of *Poria subacida*, cracked in drying.

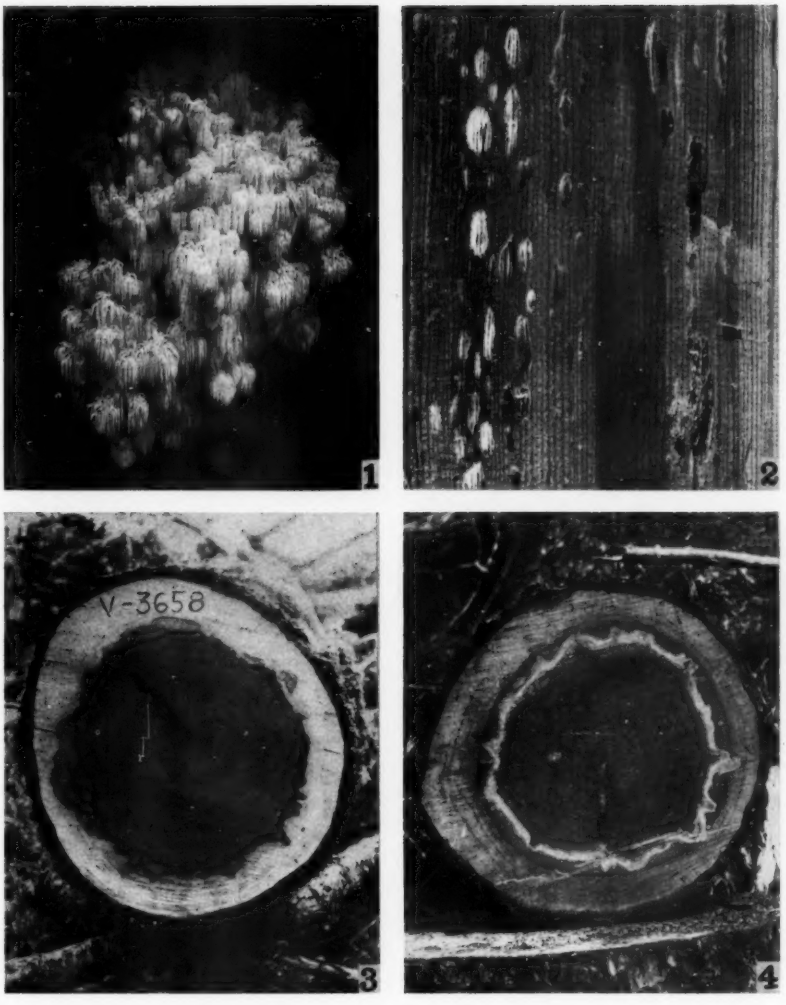
FIG. 4. White laminate butt rot caused by *P. subacida*.



Fomes pini, *Poria tsugina*, and *Poria nigrescens* on living western hemlock.

FIG. 1. Sporophore of *Fomes pini* fruiting in association with a decayed branch stub.
FIG. 2. White pitted trunk rot caused by *F. pini*.
FIG. 3. Hoof-shaped sporophores of *Poria tsugina* on western hemlock.
FIG. 4. Resupinate sporophore of *P. tsugina* on the undersurface of a branch.
FIG. 5. Fruiting bodies of *Poria nigrescens* and associated decay in western hemlock.

PLATE V

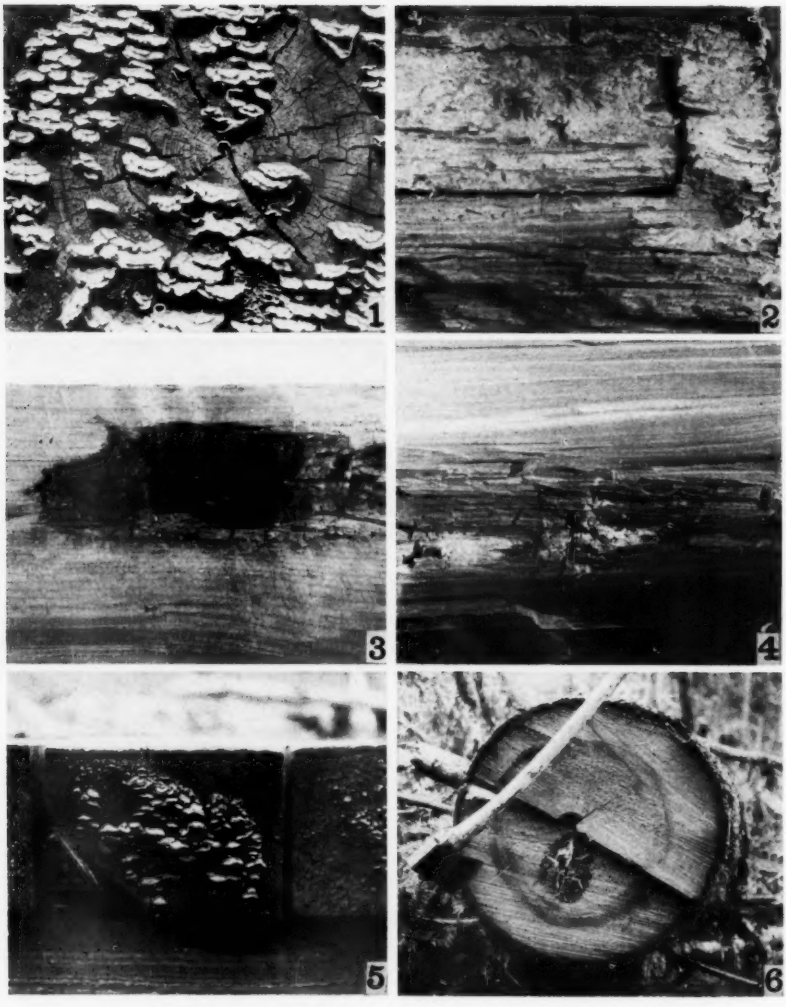


Hericium sp. on living western hemlock.

FIG. 1. Coral-like fruiting bodies of *Hericium* sp.

FIG. 2. Long-pitted rot caused by *Hericium* sp. showing the incipient stain and light colored pits, in part empty and in part filled with white aggregations of fungous and host material.

FIGS. 3 and 4. Cross sections of long-pitted rot, caused by *Hericium* sp., showing the irregular margins and isolated pockets of advanced decay.



Stereum abietinum on western hemlock.

FIG. 1. Fruiting bodies of *Stereum abietinum* on dead and down western hemlock.

FIG. 2. Advanced decay caused by *S. abietinum* showing thin wefts of mycelium.

FIG. 3. Advanced decay caused by *S. abietinum* showing an isolated pocket surrounded by what appears to be sound wood.

FIG. 4. Advanced decay caused by *S. abietinum* showing the brown cubical nature of the rot and an associated black stain.

FIG. 5. Fruiting bodies of *S. abietinum* contributing to the deterioration of western hemlock under service conditions.

FIG. 6. Advanced decay caused by *S. abietinum* showing an isolated pocket containing white mycelial accumulations.

unknown (Plate IV). The sporophores are entirely resupinate and characterized by minute pores. Color has been recorded as white when fresh, turning red immediately on bruising and dark brown or black on partial or complete drying. Color changes from white to black have been observed to occur within six hours. Similar changes are known to take place in the case of *Poria decolorans* (Schw.) Cke. Western hemlock, Sitka spruce, and western red cedar are known hosts for this fungus on the Queen Charlotte Islands.

Long-pitted Rot Caused by Hericium sp.

In the incipient stage the infected wood shows a yellowish to brownish discoloration. Later, small elongated pits may appear. The individual pits are often three-fourths of an inch in length, approximately one-eighth to one-fourth of an inch in width, and are delimited by what appears to be sound wood. The pits are generally blunt-pointed and contain white to light-yellow fibers. No zone lines have been observed. The decay appears very similar to the white-pitted rot caused by *Fomes pini*. In the case of long-pitted rot, however, the individual pits are longer and often light-yellow in color, the decay presents a more pronounced contrast with the uninfected portions, and irregular lines or pockets may be formed adjacent to the normal wood (Plate V).

Diameter Relationships

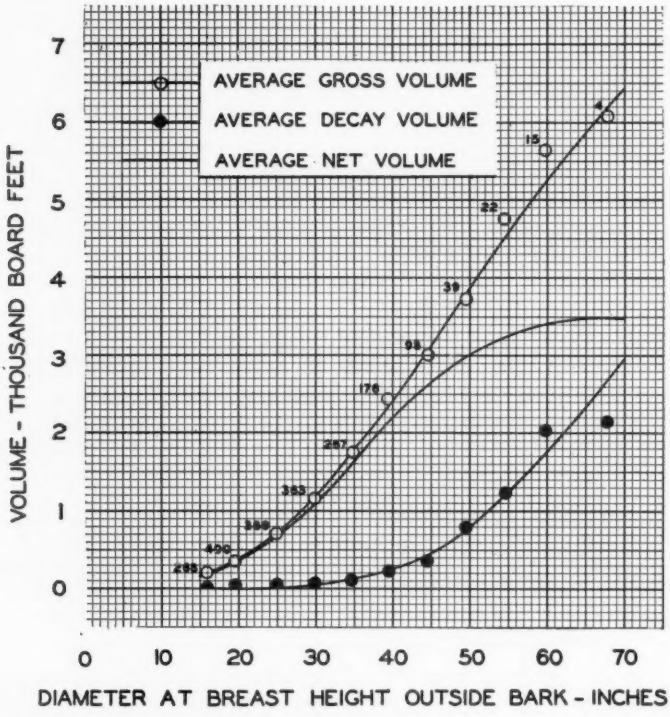
Decay in Relation to Gross Volume

As a prerequisite to the analysis of decay in relation to diameter, trees were separated into two groups, living and dead. This procedure appears to conform with general forest inventory practice in old-growth timber. A total of 277 dead trees, all subsequently classed as culls, were rejected on this basis. Additional cull trees were encountered within the group of residuals. Although certain trees in the latter group provided external indications of defect, other trees showing similar symptoms contained sufficient sound wood to warrant utilization. In view of the paucity of information relating the various external indicators of decay to the volume of associated defect, and because of the diversity of opinion in this regard, it was not considered feasible to reject other than dead trees from the present sample. Accordingly, all living trees, irrespective of known or assumed decadence, were included in the analysis. The results are shown in Text-fig. 2 and Table VII.

Relatively minor losses from heart rot were encountered in trees of less than 40 in. d.b.h. Between this diameter and 70 in., however, decay increased from 8 to 44% and from 10 to 46% in cubic and board feet respectively. Maximum values of net periodic increment were obtained at 40 in. in cubic feet and at 35 in. in board feet. It is to be noted that these data apply only to trees with green foliage.

On a stand basis, i.e. including both living and dead trees, decay was found to be of significance at all diameters. Curved values in cubic feet derived

from the basic data have shown that decay increased from 5% at 15 in. to 60% at 70 in. In board feet the corresponding values were 7 and 71% respectively.



TEXT-FIG. 2. Relationship between diameter and gross volume, decay volume, and net volume in board feet for living western hemlock on the Queen Charlotte Islands. Average site index 110. Average deviations: gross volume 24.2%, % decay 8.3, net volume 27.2%.

Although it has been shown that decay increases progressively with diameter (Text-fig. 2), it is to be noted that extensive variations in the case of individual trees were encountered. Thus, the average deviation recorded in the case of living trees was 8.3%. Further information in this regard is presented in Table VIII. It has been found that the percentage of trees free from rot decreases progressively with increasing diameter, and conversely, that there is a cumulative risk of infection with increasing diameter. It is further evident that average cull percentages do not provide reliable estimates of decay in individual trees. In this way an average loss of approximately 20% has been indicated at 50 in. (Table VII). At this same diameter, however, 26% of the trees were found to be free from rot and 16% to contain

TABLE VII

THE RELATIONSHIP BETWEEN DIAMETER AND PERCENTAGE OF DECAY AND NET MERCHANTABLE VOLUME IN 2041 LIVING WESTERN HEMLOCK ON THE QUEEN CHARLOTTE ISLANDS

(Curved values)

Diameter breast height	No. of trees	Cubic feet			Board feet		
		Average gross volume	Percentage of decay	Average net volume	Average gross volume	Percentage of decay	Average net volume
15	268	40	1.5	39	180	2.2	176
20	400	90	2.2	88	390	4.1	374
25	389	155	3.2	150	730	4.8	695
30	363	240	4.6	229	1175	6.4	1100
35	267	340	5.9	320	1800	7.5	1665
40	176	450	7.6	416	2450	10.2	2200
45	98	570	11.4	505	3170	14.2	2720
50	39	700	17.8	575	3870	20.7	3070
55	22	830	24.1	630	4570	28.8	3290
60	15	970	30.9	670	5250	34.3	3450
65	2	1110	37.8	690	5875	40.8	3475
70	2	1250	44.0	700	6500	46.2	3500

greater than 50% of their volume in defective wood. Under such circumstances it is essential that average cull factors be applied to samples of sufficient size to include the normal range in variation in amount of decay.

TABLE VIII

FREQUENCY DISTRIBUTION OF LIVING WESTERN HEMLOCK ON THE QUEEN CHARLOTTE ISLANDS CONTAINING GREATER OR LESSER AMOUNTS OF DECAY

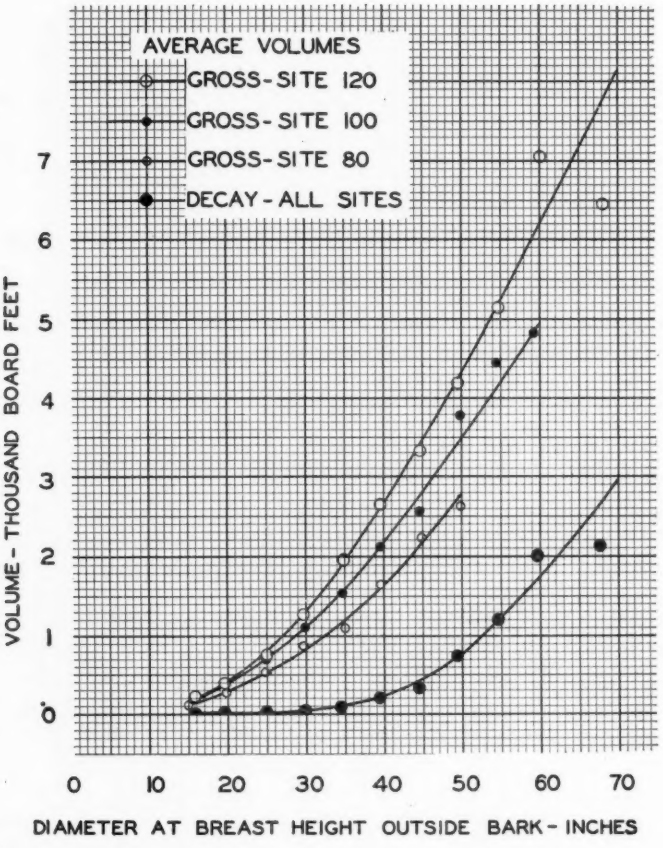
(Basic data)

Diameter breast height	Percentage of trees in class having:				
	Measurable amounts of decay	0% decay	1-25% decay	26-50% decay	51-100% decay
15	19	81	17	Trace*	2
20	22	78	17	3	2
25	37	63	30	3	4
30	43	57	35	6	2
35	57	43	49	6	2
40	67	33	56	7	4
45	72	28	55	12	5
50	74	26	38	20	16
55	86	14	41	27	18
60	100	0	40	20	40

* *Trace, less than 1.0%.*

Decay in Relation to Site

An analysis of decay in relation to site failed to reveal any significant difference in the average volume of decay between Sites 100 and 120. Consistent trends were obtained, however, in the case of gross volume. Accordingly, it was considered that site, as measured by the maximum height of dominant trees at maturity, exerts no appreciable or consistent influence on the relation between average volume of decay and diameter. It is suggested that differences in loss in percentage of volume may be attributed primarily to differences in gross volume (Text-fig. 3, Table IX). Although these data apply only to trees with green foliage it is evident that extensive losses may be



TEXT-FIG. 3. Relationship between diameter, gross volume, and decay volume by site in board feet for western hemlock on the Queen Charlotte Islands. Curves based on 1162 trees, Site 120; 752 trees, Site 100; 124 trees, Site 80. Average deviations in gross volume: Site 120, 19.1%; Site 100, 19.1%; Site 80, 18.1%.

TABLE IX

THE RELATIONSHIPS BETWEEN DIAMETER AND PERCENTAGE OF DECAY AND NET MERCHANTABLE VOLUME TO A 10-IN. TOP IN 2041 LIVING WESTERN HEMLOCK ON THE QUEEN CHARLOTTE ISLANDS

(Curved values)

Diameter breast height	No. of trees	Board feet			Cubic feet		
		Average gross volume	Percentage of decay	Average net volume	Average gross volume	Percentage of decay	Average net volume
Site 80							
15	24	110	3.6	104	30	2.0	29
20	25	270	5.9	254	65	3.1	63
25	38	510	6.9	475	115	4.3	110
30	24	820	9.1	745	175	6.3	164
35	7	1210	11.2	1075	245	8.2	225
40	3	1670	15.0	1420	330	10.3	296
45	1	2200	20.4	1750	430	15.1	365
50	2	2790	28.7	1990	550	22.7	425
Site 100							
15	81	160	2.5	156	40	1.5	39
20	157	400	4.0	384	85	2.4	83
25	143	720	4.9	685	145	3.4	140
30	132	1110	6.8	1035	220	5.0	209
35	99	1600	8.4	1465	315	6.3	295
40	65	2160	11.6	1910	420	8.1	386
45	37	2810	16.0	2360	535	12.1	470
50	17	3510	22.8	2710	660	18.9	535
55	12	4210	28.5	3010	795	25.2	595
60	9	4950	36.4	3150	940	31.9	640
Site 120							
15	163	190	2.1	186	40	1.5	39
20	218	410	3.9	394	90	2.2	88
25	208	790	4.4	755	165	3.0	160
30	207	1300	5.8	1225	265	4.2	254
35	161	1950	6.9	1815	375	5.3	355
40	108	2700	9.2	2450	495	6.9	461
45	60	3500	12.8	3050	625	10.4	560
50	20	4350	18.4	3550	760	16.4	635
55	10	5260	22.8	4060	905	22.1	705
60	6	6180	29.1	4380	1060	28.3	760
65	0	7140	33.6	4740	1225	34.3	805
70	1	8160	36.8	5160	1400	39.3	850

anticipated in the larger diameter classes and on the poorer sites. Thus, on Site 80 decay increased from approximately 4% to 29% between 15 and 50 in. Progressively smaller cull factors were encountered with increasing site quality. Within the diameter range just mentioned decay increased from

2 to 23% on Site 100 and from 2 to 18% on Site 120. The diameter distribution of trees on the better sites provided for an extension of data to 60 in. in Site 100 and to 70 in. on Site 120.

Graphical analyses of the basic data have indicated consistent trends of increasing infection with diameter on all sites (Table X). Existing evidence

TABLE X

THE RELATIONSHIP BETWEEN DIAMETER AND DISEASE INFECTION BY SITE CLASSES FOR LIVING WESTERN HEMLOCK ON THE QUEEN CHARLOTTE ISLANDS

(Curved values)

Diameter breast height	Percentage of infected trees			
	Site 80	Site 100	Site 120	All sites
15	5	8	23	15
20	18	20	31	25
25	30	30	39	34
30	43	40	48	44
35	56	51	56	53
40	68	62	65	63
45	82	73	73	73
50	100	83	82	82
55	—	94	90	92
60	—	100	98	100
65	—	—	100	100
70	—	—	100	100

would further indicate that the majority of trees on good sites become infected at smaller diameters than those on poor sites. Selected trees, however, may remain free from infection for longer periods.

Decay in Relation to Grade

In view of the large diameters and related growth characteristics of western hemlock on the Queen Charlotte Islands, it has been considered desirable to relate decay on a qualitative as well as a quantitative basis. In assigning grades for this purpose logs were required only to be of sufficient diameter and length and to contain a minimum of knots, branches, and spiral grain to qualify for Grades 1 or 2. All remaining logs were classified as Grade 3. Cull logs were assigned a numerical grade but the gross volumes were reduced according to the amount of internal defect. No reductions in grade were made for ring shake, pitch pockets, breakage, or related natural defects, owing to the observed variation in incidence and importance of features of this nature and the difficulty of making reliable estimates for volume under field conditions. Similarly, decay was considered to constitute a defect permissible in any grade. In view of the method of grading, some qualification of the volume data may be required. Thus, volumes similar to those indicated as potential net volume could be anticipated in the absence of ring shake, pitch pockets, and breakage, and equivalent gross volumes could be realized in the

absence of these latter factors and decay. The relationships between diameter and potential yield by grade, established on the foregoing basis, are presented in Table XI. It is to be noted than an average of 23% of the total volume

TABLE XI

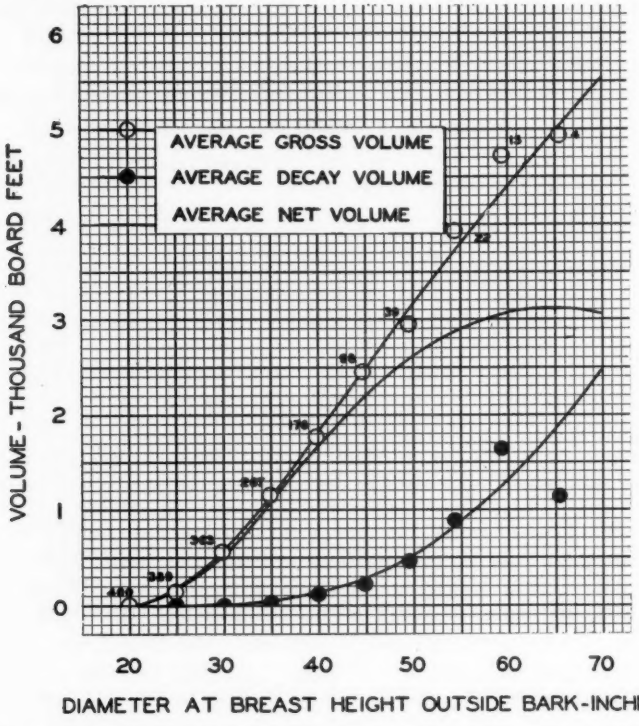
THE RELATIONSHIP BETWEEN DIAMETER AND POTENTIAL GROSS YIELD IN GROSS VOLUME BY GRADE FOR LIVING WESTERN HEMLOCK ON THE QUEEN CHARLOTTE ISLANDS

(Basic data)

Diameter breast height	Percentage of potential gross volume contained in:			
	Grade 1	Grade 2	Grades 1 and 2	Grade 3
15	—	—	—	100.0
20	—	0.4	0.4	99.6
25	—	9.3	9.3	90.7
30	0.7	41.0	41.7	58.3
35	13.1	48.6	61.7	38.3
40	32.8	39.3	72.1	27.9
45	49.9	26.7	76.6	23.4
50	53.1	21.5	74.6	25.4
55	52.5	25.6	78.1	21.9
60	63.5	15.5	79.0	21.0
65	60.5	20.4	80.9	19.1
70	66.0	21.7	87.7	12.3
Weighted average	23.5	33.0	56.5	43.5

was contained in Grade 1 wood. In view of the diameter requirements of this class, all measurable volumes were confined to trees in excess of 30 in. d.b.h. A substantial increase in Grade 1 material was recorded between 35 and 50 in. and a much slower increase beyond the latter diameter. One-third of the gross volume was contained in Grade 2 logs, or a total of 56% in potential sawlog material, Grades 1 and 2 combined. The decreasing percentage of Grade 2 material above 35 in. may be related in large part to the assignment of an increasing proportion of the total sawlog material to Grade 1. An average of 44% of the gross volume was contained in Grade 3. Owing to the arbitrary influence of diameter on the higher grades, most of the Grade 3 volume was contained in diameter classes below 35 in. It is to be noted (Text-fig. 4 and Table XII) that average gross volume, percentage of decay, and average net volume increase progressively with diameter, and that appreciable losses were recorded in all grades. The extensive losses recorded in the case of Grade 3 may be attributed in part to the more frequent occurrence of branches, the greater length exposed to infection, and the occurrence of broken tops, particularly in the larger diameter and height classes. Although the average gross volume by grade increases progressively with diameter, a study of net periodic increment indicates that it is not economically feasible to reserve western hemlock for the period required to reach advanced diameters (Table XIII). Thus, maximum net periodic increments were obtained at

45 in. in the case of Grade 1 and at 40 in. in the case of Grade 1 and 2 combined. Beyond these diameters the net periodic increments were found to decrease progressively up to 70 in. At this diameter, moreover, the decay increment in board feet exceeded that of gross volume and a corresponding reduction in net yield was in evidence.



TEXT-FIG. 4. Relationship between diameter and potential gross volume, decay volume, and potential net volume of Grade 1 and Grade 2 wood combined, in living western hemlock on the Queen Charlotte Islands.

Age Relationships

The Evaluation of Tree Age

Curved values derived from the basic data have indicated a progressive trend in age with increasing diameter. Further analyses, however, have shown that excessive variations in age were encountered (Table XIV). The average deviation for the entire sample amounted to 53 years and standard errors in excess of 100 years were encountered in certain of the larger diameter classes. Under such circumstances it is evident that diameter alone provides an inadequate basis for the accurate determination of tree age.

TABLE XII

THE RELATIONSHIP BETWEEN DIAMETER AND PERCENTAGE OF DECAY AND AVERAGE NET VOLUME BY GRADE IN LIVING WESTERN HEMLOCK ON THE QUEEN CHARLOTTE ISLANDS

(Curved values)

Diameter breast height	Grade 1 wood			Grade 1 and Grade 2 wood			Grade 3 wood		
	Potential gross volume	Percentage of decay	Average net volume	Potential gross volume	Percentage of decay	Average net volume	Potential gross volume	Percentage of decay	Average net volume
Cubic feet									
15	—	—	—	—	—	—	40	1.5	39
20	—	—	—	Trace	—	Trace	90	2.2	88
25	—	—	—	30	2.0	29	125	3.2	121
30	2	Trace	2	110	2.7	107	130	6.2	122
35	55	3.6	53	205	3.9	197	135	8.9	123
40	155	4.5	148	310	5.2	295	140	12.9	122
45	265	7.2	246	425	8.0	391	145	21.4	114
50	380	13.2	330	540	13.9	465	160	31.2	110
55	490	18.9	397	660	19.7	530	170	41.2	100
60	600	26.0	444	785	26.2	579	185	50.8	91
65	700	33.4	466	915	32.6	617	195	62.6	73
70	800	40.0	480	1040	38.5	640	210	71.4	60
Board feet									
15	—	—	—	—	—	—	180	2.2	176
20	—	—	—	Trace	—	Trace	390	3.6	376
25	—	—	—	180	2.2	176	550	5.5	696
30	5	Trace	5	565	3.6	545	610	8.2	1105
35	350	5.7	330	1155	5.5	1091	645	12.4	1656
40	850	8.2	780	1795	7.8	1655	655	18.3	2190
45	1480	11.8	1305	2485	11.7	2194	685	24.1	2714

TABLE XII—*Concluded*

THE RELATIONSHIP BETWEEN DIAMETER AND PERCENTAGE OF DECAY AND AVERAGE NET VOLUME BY GRADE IN LIVING WESTERN HEMLOCK ON THE QUEEN CHARLOTTE ISLANDS—*Concluded*

(Curved values)

Diameter breast height	Grade 1 wood			Grade 1 and Grade 2 wood			Grade 3 wood		
	Potential gross volume	Percentage of decay	Average net volume	Potential gross volume	Percentage of decay	Average net volume	Potential gross volume	Percentage of decay	Average net volume
Board feet—Concluded									
50	2110	17.5	1740	3145	16.8	2616	725	31.7	3111
55	2740	23.9	2085	3795	23.3	2912	775	40.0	3377
60	3330	30.6	2310	4410	29.9	3092	840	51.2	3502
65	3870	37.7	2410	4960	37.2	3115	915	63.4	3450
70	4400	45.5	2400	5550	45.9	3070	1000	73.7	3250

TABLE XIII

RELATION BETWEEN DIAMETER AND NET PERIODIC INCREMENT BY GRADE IN LIVING WESTERN HEMLOCK ON THE QUEEN CHARLOTTE ISLANDS

(Curved values)

Diameter breast height	Net periodic increment					
	Cubic feet			Board feet		
	Grade 1	Grades 1 and 2	All grades	Grade 1	Grades 1 and 2	All grades
15	—	—	39	—	—	176
20	—	—	49	—	—	200
25	—	29	62	—	176	320
30	2	78	79	5	369	409
35	51	90	91	325	546	551
40	95	98	96	450	564	534
45	98	96	89	525	539	524
50	84	74	70	435	422	397
55	67	65	58	345	296	266
60	47	49	40	225	180	125
65	22	38	20	100	23	−52
70	14	23	10	−10	−115	−200

TABLE XIV

THE RELATIONSHIP BETWEEN DIAMETER AND AGE OF WESTERN HEMLOCK ON THE QUEEN CHARLOTTE ISLANDS

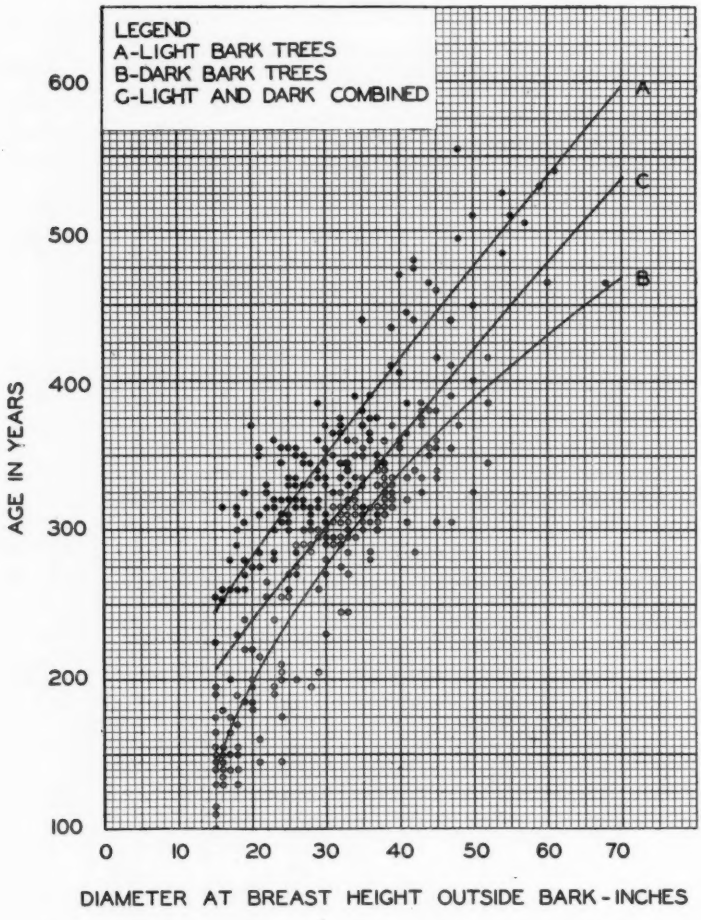
(Basis 2318 trees)

Diameter at breast height	Number of trees	Average age, curved	Standard error of individual observations
15	278	195	50.8
20	428	225	61.8
25	441	260	71.5
30	411	295	53.4
35	309	325	71.7
40	212	360	70.1
45	125	395	78.3
50	50	430	70.5
55	32	465	70.1
60	18	495	82.9
65	3	530	128.2
70	2	565	143.5

Note: *Average deviation 52.7 years.*

To provide a further index of tree maturity, 345 trees selected at random were segregated into categories of light and dark bark. Trees of the former group were characterized by a thin, light to dark gray, scaly bark; those of the latter group displayed a thick bark, dark brown in color, and deeply furrowed or ridged in texture (Plate I, Figs. 3 and 4). Trees of intermediate

coloration were not included in the present analysis. Although trees of both categories were represented in all age classes from 100 to 500 years, it was found that bark coloration and tree vigor were closely related (Text-fig. 5).



TEXT-FIG. 5. Relationship between age and diameter in light bark and dark bark western hemlock on the Queen Charlotte Islands. Basis 345 trees, Site 100.

Bark categories, superimposed on the diameter–age relationship reduced the total variance in age by more than 50%. Although over 40% of the variance was attributed to unknown factors, observational evidence indicates that stand density and site may serve to reduce the remaining variance to an

acceptable minimum. In view of the importance in forest management of defining stand age as accurately as possible, further studies of this nature would appear warranted.

Infection and Age

The relationship between incidence of infection and age is presented in Table XV. Of the 2318 trees examined, 1120, or 48.3%, contained measur-

TABLE XV

THE RELATIONSHIP BETWEEN AGE AND INCIDENCE OF INFECTION IN WESTERN HEMLOCK ON THE QUEEN CHARLOTTE ISLANDS

(Basic data)

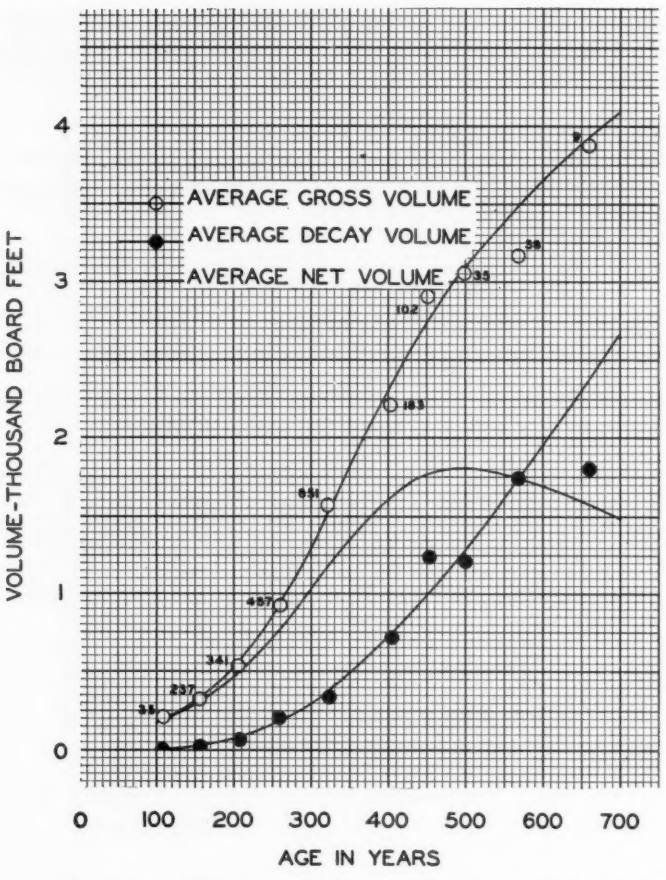
Age class	Average age	Number of trees	Number of trees with decay	Percentage of trees with decay
76 – 125	102	35	2	5.7
126 – 175	154	237	17	7.2
176 – 225	201	341	93	27.3
226 – 275	253	487	226	46.4
276 – 325	299	537	305	56.8
326 – 375	348	314	179	57.0
376 – 425	399	183	142	77.6
426 – 475	449	102	84	82.4
476 – 525	496	35	28	80.0
526 – 575	548	22	19	86.4
576 – 625	594	16	16	100.0
626 – 675	649	7	7	100.0
676 – 725	686	2	2	100.0
Total or average	287	2318	1120	48.3

able amounts of decay. The percentage of trees with rot increased progressively with age from approximately 6% at age 100 to 100% at age 600. These data support previous evidence in regard to the cumulative risk of infection with age.

Quantitative Recovery

On the basis of curved values (Text-fig. 6 and Table XVI) relatively minor losses were recorded in trees less than 200 years of age. Decay did not become appreciable until an approximate age of 300 years. Beyond this heart rot losses increased progressively to 65% at 700 years of age.

Maximum net volumes of sound wood were recorded in trees approximately 500 years old. Between 300 and 350 years there was an appreciable reduction in the net periodic increment and at 525 years individual trees became non-productive, annually losing more through the development of decay than they gained through the growth of new wood. These data indicate that those concerned with forest management should consider 300 and 500 years as the critical ages in priority cutting.



TEXT-FIG. 6. Relationship between age and average gross volume, decay volume, and net volume in board feet for living western hemlock on the Queen Charlotte Islands. Average site index 110.

Qualitative Recovery

The frequency distribution of trees contained in the present sample did not permit a reliable extension of the site class data beyond 450 years. Further qualifications of the data were necessary owing to the excessive variations encountered within most age classes. Although consistent trends were observed up to 450 years, direct application of the data would not appear warranted without further supporting evidence.

While trees on Site 120 were generally larger than those on Site 100, consistent differences in diameter and volume did not become apparent until approximately age 300. Negligible quantities of Grade 1 material were

TABLE XVI

THE RELATIONSHIP BETWEEN AVERAGE GROSS VOLUME, AVERAGE DECAY VOLUME, PERCENTAGE OF DECAY, AVERAGE NET VOLUME, NET PERIODIC INCREMENT, AND AGE OF WESTERN HEMLOCK ON THE QUEEN CHARLOTTE ISLANDS

(Curved values)

Average age	Average gross volume	Average volume of decay	Percentage of decay	Average net volume	Net periodic increment
Board feet					
100	200	5	2.5	195	—
150	325	20	6.1	305	110
200	525	50	9.5	465	160
250	875	150	17.1	725	260
300	1350	300	22.2	1050	325
350	1875	515	27.4	1360	315
400	2350	750	31.9	1600	240
450	2750	1015	36.9	1735	135
500	3100	1300	41.9	1860	65
550	3375	1625	48.9	1750	− 50
600	3625	1960	54.1	1665	− 85
650	3865	2300	59.5	1565	−100
700	4100	2650	64.6	1450	−115
Cubic feet					
100	40	1	2.5	39	—
150	67	4	5.9	63	24
200	110	10	9.1	100	37
250	172	27	15.7	145	45
300	267	50	18.7	217	72
350	350	85	24.3	265	48
400	430	123	28.6	307	42
450	500	170	34.0	330	23
500	562	220	39.1	342	12
550	621	276	44.4	345	3
600	678	333	49.1	345	0
650	730	392	53.7	338	− 7
700	780	452	57.9	328	−10

recorded on Site 80 in trees of less than 400 years of age. Substantial yields were realized on the better sites in trees older than 250 years (Text-fig. 7 and Table XVII). Thus, on Sites 100 and 120 the volume of Grade 1 material, expressed as a percentage of the total age class volume, increased from 9% at 250 years to 54% at age 600. Decay increased from 1.3% at 250 years to 33% at 600 years. Although approximately equivalent gross volumes of decay were recorded on the better sites, root rots were more prevalent on Site 120 and trunk rots were of a more serious nature on Site 100. The full significance of this latter finding in forest management has yet to be determined.

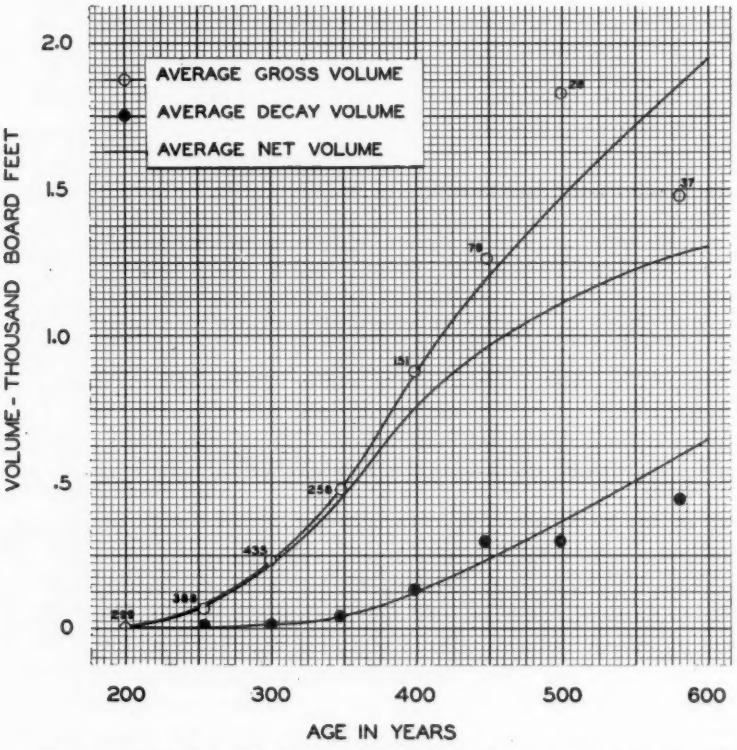
TABLE XVII

THE RELATIONSHIP BETWEEN AGE AND QUALITATIVE RECOVERY IN WESTERN HEMLOCK ON THE QUEEN CHARLOTTE ISLANDS

(Curved values: basis 1883 trees)

Age	Average gross volume	Grade 1 wood*		Decay volume	Percentage of decay	Net volume
		Average volume	Percentage of total			
200	525	5	1.0	0	0.0	5
250	875	75	8.6	1	1.3	74
300	1350	230	17.0	10	4.3	220
350	1875	490	26.1	35	7.1	455
400	2350	880	37.4	120	13.6	760
450	2750	1210	44.0	240	19.8	970
500	3100	1480	47.7	365	24.7	1115
550	3375	1730	51.2	500	28.9	1230
600	3625	1960	54.1	650	33.2	1310

* *Sites 100 and 120.*



TEXT-FIG. 7. Relationship between age and potential gross volume, decay volume, and potential net volume of Grade 1 western hemlock on the Queen Charlotte Islands. Site indices 100 and 120

TABLE XVIII

THE PREVALENCE AND RELATIVE IMPORTANCE OF THE MORE COMMON DECAYS OF WESTERN HEMLOCK IN RELATION TO AGE

Age class	*Fomes pinicola*	*Poria subacida*	*Fomes annosus*	*Stereum abietinum*	*Armillaria mellea*	*Fomes pini*
Volume of decay expressed as a percentage of total age class volume						
26 – 125	0.0	0.0	0.6	0.0	0.0	0.0
126 – 225	0.9	0.1	0.4	0.1	0.1	0.2
226 – 325	1.2	0.2	0.6	0.2	0.3	0.6
326 – 425	1.5	0.5	1.1	0.6	0.7	1.5
426 – 525	2.5	0.9	3.0	2.1	3.1	2.6
526 – 625	5.8	1.6	5.7	0.8	0.9	7.1
626 – 725	0.2	6.8	0.0	0.0	0.0	5.0
Number of infected trees expressed as a percentage of total trees in age class						
26 – 125	0.0	0.0	2.9	0.0	0.0	0.0
126 – 225	2.5	1.4	1.3	0.9	1.1	0.5
226 – 325	6.3	6.1	5.6	3.9	2.8	1.9
326 – 425	9.2	9.2	8.3	5.9	5.7	6.9
426 – 525	17.4	10.1	11.0	19.3	15.6	11.0
526 – 625	12.9	16.1	25.8	9.7	12.9	22.6
626 – 725	28.6	28.6	0.0	0.0	0.0	14.3

Decay Relationships

The relation between age and the incidence and importance of certain of the more common fungi is shown in Table XVIII. It is to be observed that there is a progressive increase with age, within the limits of reliable data, in both respects mentioned for all the species analyzed on this basis. These findings support previous evidence that the more serious nature of decay in the older age classes may be related in large part to early infection and the subsequent development of decay, rather than to the occurrence of decay-producing fungi confined to the final stages of deterioration. The present data do not support the thesis (13) that root and butt rots are of a more serious nature in trees up to approximately 300 years old or that their importance in relation to the other fungi declines in the older age classes. In view of recorded differences in the complex of decay-producing fungi, however, it is probable that considerable variation in the relative importance of specific organisms and their relation to age may occur on a regional basis.

Understory Trees

Since it is probable that trees of less than 15 in. d.b.h. will be utilized in the future as facilities for logging and transporting smaller-sized material becomes available, it was considered that information relating to the potential pulpwood volume and decay losses contained in such trees would be of interest. Accordingly, a tally was maintained of all hemlock and spruce from 6 to 14 in. in diameter. To obtain the cubic foot volumes of trees within this diameter range, 56 western hemlock were felled at a stump height of 2.0 ft. and inside bark measurements recorded at 2-ft. intervals for the total length of the tree. Cubic foot volumes were then computed in 8-ft. logs to an average top diameter inside bark of 2.6 in. (Table XIX). Volumes for understory spruce were

TABLE XIX

LOCAL VOLUME TABLE FOR UNDERSTORY WESTERN HEMLOCK ON THE QUEEN CHARLOTTE ISLANDS

(Basis 65 trees)

Diameter breast height	Average height to merchantable top (ft.)	Average gross volume (cu. ft.)
6	48	5.7
8	56	10.2
10	63	18.8
12	72	29.8
14	76	42.0

Note: *Trees selected on Site 100, and scaled in 8-ft. logs to an average top diameter of 2.6 in.*

Average deviation in gross volume: 5.5%.

considered to be equivalent to those of hemlock of the same diameter. Volume data of this nature applied to the total number of living understory spruce and hemlock are shown in Table XX. It is to be noted that an average yield

TABLE XX

BASIC DATA PERTAINING TO LIVING UNDERSTORY HEMLOCK AND SPRUCE ON THE QUEEN CHARLOTTE ISLANDS

(Basic 47 acres)

Average number of trees per acre	63	Volume per acre (cords)	
Average age (years)	140	Minimum	3.4
Average d.b.h. (in.)	9.0	Maximum	29.5
		Average	10.5

of 10.5 cords per acre was obtained. In this connection it is of interest to note that a total recovery of 10 cords per acre is considered satisfactory for pulpwood utilization in Eastern Canada (6). Present evidence indicates that heart rot losses are of negligible importance. In addition, dead trees contained an average of only 0.5 cords per acre and breakage losses were confined to the upper crown. It is evident, therefore, that almost complete utilization of the understory could be obtained.

Discussion

The present study was initiated to provide basic information relative to the pathology of western hemlock on the Queen Charlotte Islands.

It became evident at an early stage in the investigations that western hemlock was subject to attack by a complex of decay-producing fungi. In all, 27 organisms, exclusive of those apparently confined to slash and other dead material, were isolated from living trees. Few of the associated decays presented sufficient characteristics to permit their reliable separation in the field. Although 15 species were classed in a relative sense as important heart-rotting fungi, no single species was responsible for an over-all loss in the gross volume of more than 2%. All of the fungi are known to occur and to be significant in other regions. Thus, the cull condition of hemlock on the Queen Charlotte Islands cannot be attributed to the occurrence of any fungus specific to the region. The decay complex is abnormal, however, in the absence of one or more species known to be serious in hemlock and associated species on the mainland. This situation is particularly evident in the case of *Echinodontium tinctorium*, long regarded as the most injurious fungus associated with western hemlock. This fungus is not known to occur on the Queen Charlotte Islands. It is suggested that its absence may be related in part to the geographical isolation of the region under consideration. Support for this suggestion is afforded by the incidence and importance of the fungus on the opposite mainland and throughout most, if not all, of the range of hemlock in the Interior of the Province. In view of the potentialities of *Echinodontium* it is fortunate indeed that natural barriers to the normal spread of the fungus exist. It is equally fortunate that the existing barriers have not been circumvented through commercial shipments or the movement of plant parts from other areas. *Trametes serialis* Fr. and *Poria monticola* Murr., species known

to occur on Sitka spruce on the Queen Charlotte Islands and to be capable of continued development under service conditions, were not recorded on living hemlock during the present study. Reference to the literature has shown, however, that hemlock is a susceptible host. The frequent occurrence of *Stereum abietinum* in living trees and its observed incidence and importance on railroad ties, storage lumber, and in buildings indicate that an intensive study of its capabilities under varying conditions would be warranted. It should be noted that the principal fungi of local importance on spruce, *Fomes pini* and *Polyporus schweinitzii* Fr., were relatively insignificant in hemlock. The decay complex associated with western hemlock was also found to vary appreciably from that recorded for western red cedar. It is evident, therefore, that the three main forest species on the Queen Charlotte Islands require separate pathological consideration. In view of the regional variation in decay, it is further necessary to restrict the application of the present data to the region under consideration. Variations of the nature indicated stress the need for more information relating to the designation of regional boundaries and the factors contributing to the distribution, incidence, and importance of the forest fungi.

Analyses of the avenues of entrance for decay have provided information of value in forest management. Thus, the susceptibility of hemlock to scar damage and the subsequent more serious injury through decay indicates certain problems to be anticipated in selective cutting. Further, the high incidence of root infections and the development of decay in the basal portions of trees of all age classes provides an index to susceptibility to wind throw.

Qualitative evaluations of decay have been shown to provide more reliable information on potential recovery than data based on gross volume. Thus, it has been found that approximately 50% of the total decay was confined to lower grades of material, normally diverted to pulpwood utilization. Only 14% loss was recorded in Grade 1 material and 8% in Grade 2. Despite the high incidence of decay, therefore, it is evident that appreciable yields of sawlog material may be obtained.

Although the average cull factor applicable for western hemlock on a regional basis amounted to 25% of the gross volume, considerable variation among sample areas was encountered. Thus, decay varied from 15 to 45%. Under such circumstances it is evident that analyses of the factors contributing to the variation in decay would provide for more dependable inventories of sound wood recovery. Apart from the examination of representative areas of felled and bucked timber, there is perhaps no better method of estimating total stand defect than by the application of cull factors to specific classes of timber. The present study has shown that decay may be related with some degree of reliability to diameter, age, and site.

Diameter relationships provide for the direct correlation of pathological data to forest inventory procedures. For example, local volume tables have been prepared for Sites 80 to 120, indicating the probable net volume recovery by grade. Decay was found to increase progressively with diameter and to

be of greater consequence on the poorer sites. It is apparent, therefore, that higher yields will be obtained from trees of larger diameters on the better sites than from trees of similar diameters on less favorable sites. Hemlock was found to attain its maximum net periodic increment between 35 and 40 in. In spruce it appears that increasing yields may be obtained up to 70 in. In the latter species, moreover, previous investigations indicate consistently greater yields of Grade 1 material at all diameters. Although the greater unit value of spruce suggests that primary consideration should be given to this species, the appreciable volumes of hemlock contained in mixed stands would require equal, if not greater, consideration in forest management. Support for this opinion is gained through an appreciation of the more serious nature of decay in hemlock and the more rapid deterioration of mature stands.

Hemlock was found to reach an advanced stage of maturity with 50% of the gross volume in age classes in excess of 300 years. Individual trees over 700 years of age were recorded. Decay was found to increase progressively with age and to become appreciable at 300 years of age. Beyond 525 years individual trees became nonproductive, annually losing more through the development of decay than they gained through the growth of new wood. These data indicate that an appreciation of the volumes associated with trees at the critical ages of 300 and 500 would provide data essential in forest management. Unfortunately there appears to be no reliable method, short of increment analysis, to determine the ages of standing trees. Owing to the decadence and size of hemlock in the region under consideration, the extensive application of this method would not be feasible. The relation between tree age and diameter has been shown to be subject to excessive variation and is of doubtful practical value. Some promise is indicated, however, in the interpretation of bark color. Further analyses in this regard appear warranted.

Evidence has been provided to demonstrate that a substantial volume of pulpwood may be obtained through the utilization of trees from 6 to 14 in. in diameter. Heart rot losses were found to be negligible and it has been shown that an average net volume recovery of 10.5 cords per acre could be derived from stands of this class. Maximum recoveries of 29.5 cords per acre were recorded and it is probable that even greater yields could be obtained.

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ON THE MORPHOLOGY, PHYLOGENY, AND TAXONOMY OF THE LICHEN GENUS *STEREOCAULON*[1]

By I. Mackenzie Lamb[2]

Abstract

Comparative morphological and anatomical studies on the fruticose lichen genus *Stereocaulon* show that the pseudopodetial structures originate in two distinct ways, according to which it is proposed to divide the genus into two new subgenera, *Holostelidium* and *Enteropodium*. These subgenera are further divided, on a phylogenetic basis, into sections and subsections, some of which are adaptations of previously existing groupings. A phytogeographical analysis of the present day distribution of the species confirms the phylogenetic validity of the proposed subdivisions, and shows that the subgenus *Holostelidium* originated in the southern hemisphere, while the subgenus *Enteropodium* is of boreal origin. An attempt is made to reconstruct the hypothetical ancestral crustaceous prototype, which approximates closely to certain forms of *Toninia* (Catillariales). The affinities of *Stereocaulon* are therefore with the Lecideaceae, and not with the Cladoniaceae, where it is commonly placed. The chemical compounds produced by *Stereocaulon* species are enumerated, and in order to simplify taxonomy in lichens generally, it is proposed to regard morphologically indistinguishable but chemically different individuals as chemical strains, and not as distinct species as has been the previous common practice.

Introduction

Almost a century has now gone by since Th. Fries published his classical *Monographia Stereocaulorum et Pilophororum* (13), in which he described in his characteristic masterly fashion all the species known at that time. Like all his other publications, this work has stood the test of time and continues to this day to be an indispensable work of reference.

Important contributions to our knowledge of the exotic species were made shortly afterwards by Nylander in his *Synopsis Lichenum* (32), in which a number of new species were recognized and enumerated.

No further noteworthy publication on the taxonomy of the genus was made until 1910, when Riddle produced an interesting study on the North American species, defining accurately for the first time the fundamental types of phyllocladia (40). In 1923 Savicz contributed a short paper in Russian on the species found in Kamtchatka (42). Du Rietz, in 1926, published a note on the Scandinavian species of the genus, with a key to their determination and a new subgeneric division founded on the characters of the apothecia and the phyllocladia (9).

With the appearance of Magnusson's *Studies on Boreal Stereocaula* in 1926, however, it first became possible to obtain critical determinations of the European species, and this continues to be the basic work of reference for students of the genus in Europe (27). Magnusson's data have been incorporated and in some respects amplified by Frey in his treatment of the genus

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Contribution from the National Herbarium, National Museum of Canada, Ottawa.
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in Rabenhorst's Kryptogamenflora (10), which is rendered even more useful by a series of very good habit sketches and photographs.

The exotic species have been dealt with by Dodge in his *Synopsis of Stereocaulon with notes on some exotic species* (6); this paper being based to a large extent on manuscript notes made by Riddle in various European herbaria in preparation for a proposed monograph of the genus which for various reasons unfortunately had to remain uncompleted. Although Dodge's synopsis makes no claim to be more than an enumeration, without detailed descriptions, the critical notes on the type specimens of many of the exotic species makes it nevertheless a work of very considerable value.

In 1938 G. T. Johnson published an important paper on the cephalodia of *Stereocaulon* and their taxonomic significance (19). The data presented by him are dealt with in some detail in the following pages.

Japanese species of the genus were treated by Satô in the publication (in Japanese) of Nakai and Honda called *Nova Flora Japonica* (41), with good text figures illustrating the morphological and anatomical characters. Descriptions of some Japanese species have also been given in a paper by Johnson (20).

Like Riddle, the present author was fortunate in having the opportunity of examining the type specimens of nearly all the described species in the herbaria of Uppsala, Helsinki, Paris, Genève, Wien, etc., and received also from various institutions and private workers a large amount of other material for revision. In addition, he was able to study a number of species in the living state in Europe, North and South America, and Antarctica. Much work however still remains to be done before the genus can be presented in a more or less final monographic form. As yet many species are known only from the original gathering or from a few specimens only, which do not allow the complete amplitude of variation to be stated. Not only more herbarium material is necessary to remedy this deficiency, but also further field studies of the species in the living condition must be carried out, along the lines of J. W. Thomson's experiments on *Peltigera* (45). The admonition of Nylander in Ann. Sci. Nat., Bot., ser. 4, XI (1859) 264 applies with particular force to the plastic genus *Stereocaulon:* "Neque unquam in studio Lichenum praetervideatur, species eorum formas saepissime sat vagas et aspectum praebere instabilem plerumque a loco vel substrato pendentes."

In the present paper an attempt is made to evaluate the phylogenetic significance of the various vegetative and reproductive structures met with in *Stereocaulon*, and then to use the knowledge thus gained to evolve a new taxonomic subdivision of the genus based on phylogenetic principles. The problem of "chemical species" is also dealt with, not only as it affects *Stereocaulon* in particular, but also among lichens in general, and some proposals are put forward which, if generally accepted, may afford a means of recording differences in chemical constitution without throwing an unnecessary burden on formal taxonomy.

Origin and Development of the Podetia (Pseudopodetia)

The structures commonly known as podetia in fruticose lichens may be derived in more than one way from the ancestral crustose condition. They may be of carpogenic origin, formed by the elongation of the hypothecial and parathecial tissues of the apothecium (German "Fruchtstiel"), sometimes subsequently secondarily covered by assimilative thalline tissue, as was claimed by Vainio (47, 48, 49) to be the case in *Cladonia*; or they may arise by the elongation into columnar form of entire thalline areolae or verrucae (German "Lagerstiel"). Vainio (47, 48) and Magnusson (27) consider the podetia of *Stereocaulon* to be of the latter type, for which Vainio (48) originated the term "pseudopodetia", to distinguish them from podetia in the strict sense, i.e. carpogenic outgrowths. Frey (10) has considered it possible that the podetia may be of different ontogenetic origin, not only in different genera, but also within the same genus.

Whether truly carpogenic podetia ("Fruchtstiele") occur in *Stereocaulon* is very much to be doubted. In such a case the phyllocladia would have to be of secondary origin, derived from a subsequent invasion of the lengthened apothecial stalk by thalline tissues, such as takes place in *Baeomyces* (Tobler (46)). Examination of juvenile conditions of a number of *Stereocaulon* species, both boreal and exotic, has failed to reveal any development of this kind.*

That somatogenic or thalline podetia occur in *Stereocaulon* is however abundantly proved, the actual process of development by elongation of parts of the primary thallus having been observed in a number of species. This is very obvious in some of the dwarf species with a persistent crustose primary thallus, such as *condensatum*, *pileatum*, *octomerellum*, and *supervestiens*. Field observations on the highly evolved *St. ramulosum* also proved that its podetia are of purely thalline origin. *St. ramulosum* usually shows no traces of primary thallus, but on one occasion its complete development was observed by the

* *No special study has been made of podetial development in the genus* Pilophoron, *which is usually regarded as closely related to* Stereocaulon; *but outward inspection of such species as* P. aciculare *and* P. robustum *indicate that their podetia are probably of carpogenic origin, as in* Baeomyces. *This view is further supported by the fact that in a Japanese species,* P. nigricaule *Satô, the dark hypothecium is continued downwards as a subchondroid brown-blackish core from top to bottom of the podetium (Satô in J. Japan. Botany, XVI, p. 173. 1940).* Pilophoron *would therefore seem to be more closely related to* Baeomyces *than to* Stereocaulon, *in spite of the occurrence of cephalodia.*

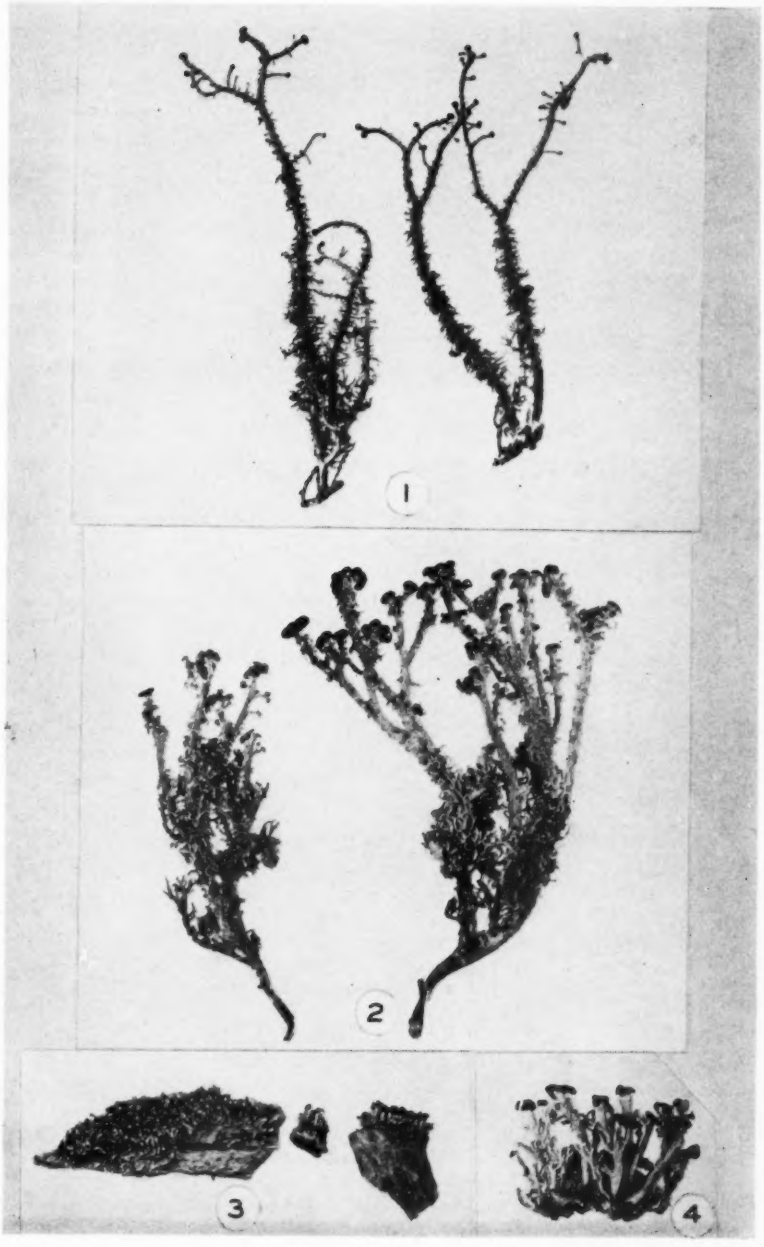
(All figures on this plate natural size)

FIG. 1. *Stereocaulon ramulosum* (Sw.) Räusch. A specimen from N.W. Argentina, Catamarca, Laguna del Tesoro, coll. I. M. Lamb, 1948 (No. 5707).

FIG. 2. *Stereocaulon Argus* Hook. f. & Tayl. emend. Th. Fr. A specimen from Argentine Patagonia, Rio Negro, Frias Glacier, coll. I. M. Lamb, 1950 (No. 6088).

FIG. 3. *Stereocaulon caespitosum* Redgr. A syntype specimen from New Zealand, Dunedin, Mt. Maungatua, coll. J. S. Thomson (No. 1361) in Herb. Botany Division, Wellington, N.Z.

FIG. 4. *Stereocaulon curtum* (Räs.) M. Lamb. A specimen from Argentine Patagonia, Rio Negro, Frias Glacier, coll. I. M. Lamb, 1950 (No. 5797).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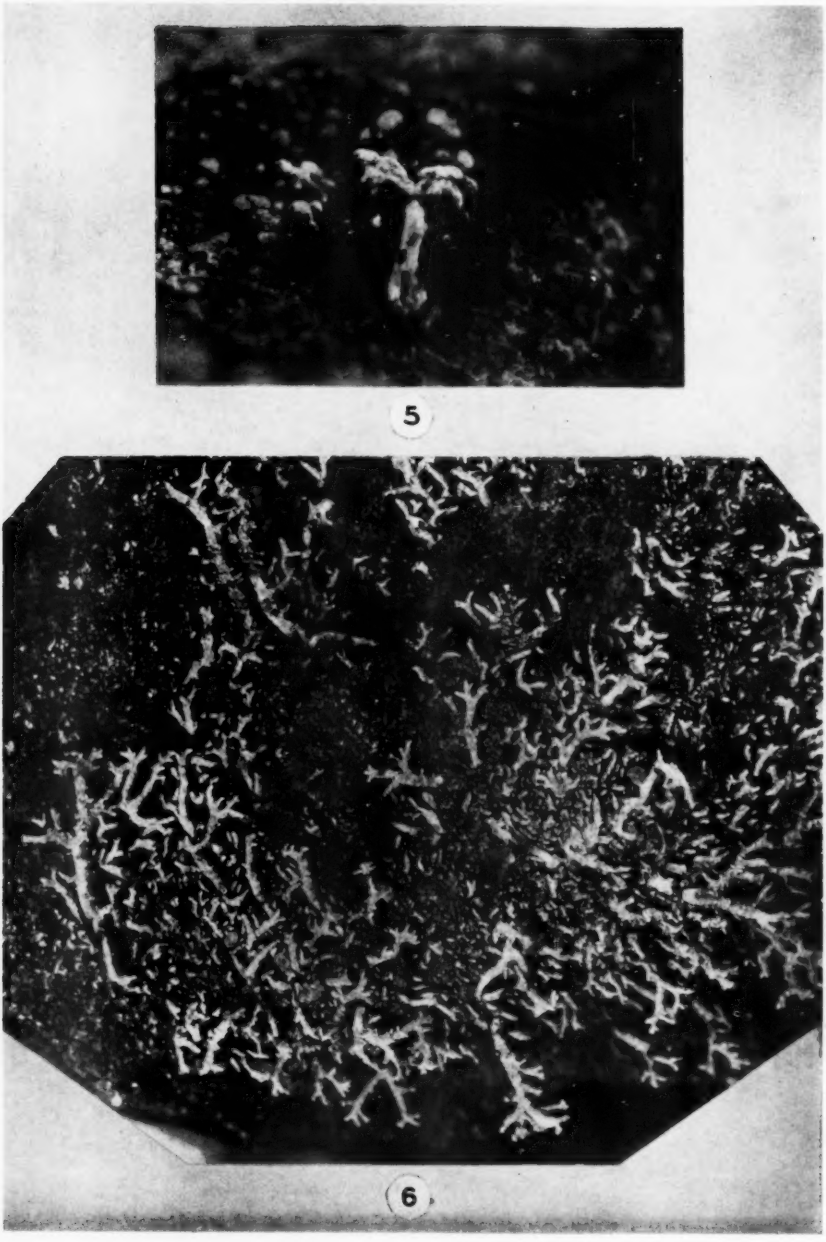

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6

author in N. W. Argentina; the primary thallus consisted of a thin, discontinuous, granulate crust, some of the granulae of which soon grew out into papillar form and subsequently by elongation into terete, saxicolous, coralloid phyllocladia similar to those on the podetia. These primary phyllocladia then became larger and commenced to branch, and in this way became gradually converted into small, dichotomously ramifying, corticate podetia (Pl. II, Fig. 6). Finally these small podetia began to throw out the finer lateral phyllocladial branchlets characteristic of the species. Cephalodia appeared on the podetia at a very early stage, while they were still in the small, dichotomously branched condition, but apothecia were formed only when they had reached their full stature and were provided with secondary lateral phyllocladial branchlets. A similar process of development was observed in a specimen of *St. claviceps* in the Stockholm Museum herbarium, collected in Japan by Almquist intact on the lump of lava rock upon which it had been growing.

The peculiar New Zealand species *caespitosum* and *gregarium* show persistence of a juvenile state of development in thalline characters, the podetia being nothing more than enlarged saxicolous primary phyllocladia which remain more or less unbranched and columnar; nevertheless, apothecia are abundantly produced at their apices, this apparently being a case of the pushing back of the reproductive cycle to an embryonic stage of somatic development (neoteny). Pl. I, Fig. 3 shows part of the syntype specimen of *St. caespitosum*; the simple, digitate podetia are covered from base to apex with a continuous layer of cortex with underlying symbiotic algae. A connection between this persistently juvenile podetial development and the fully evolved, intricately branched *ramulosum*-type is afforded by a South American species, *St. curtum* (Räs.). Here branching of the podetia takes place to a limited extent, and while the upper parts of the podetia retain their covering of continuous cortex with underlying symbiotic algae, the basal parts tend to become denuded of these layers, exposing the naked central cylinder of the podetium (Pl. I, Fig. 4).

The progressive loss of the cortex and algal stratum from the podetia becomes marked in the more highly developed and richly branching species, such as *St. ramulosum*, in most varieties of which these layers have become almost entirely lost on the podetia, and tend to persist only on the finest branches (phyllocladioid branchlets), which are copiously developed and take on the function of specialized assimilative organs (Pl. I, Fig. 1). In *St. Argus*

FIG. 5. *Stereocaulon botryosum* Ach. emend. Frey. Early stage of pseudopodetial development in a specimen from Alaska, Umiat, Colville River, coll. G. A. Llano, 1949 (No. 567). × 10.

FIG. 6. *Stereocaulon ramulosum* (Sw.) Räusch. Early stages of development from primary thallus in a specimen from N. W. Argentina, Catamarca, Laguna del Tesoro, coll. I. M. Lamb, 1948 (No. 5718). × 5.

the function of assimilation is carried on by algae both in the corticate podetia and in phyllocladioid branchlets (Pl. I, Fig. 2), and so this species in its podetial development occupies a position intermediate between *St. curtum* and *St. ramulosum*.

In the above series of species we can see a more or less continuous line of phylogenetic development of the podetium arising from a presumed ancestral crustaceous condition in accordance with the scheme represented diagrammatically in Text-fig. 6 (p. 562). It will be noted that in the development of the podetia by columnar elongation of the primary thalline bullae or areolae, *all the tissues of the latter take part in the formation of the column.* This type of development is found in the species cited above and in *all the species of Stereocaulon having terete-coralloid branchlet-phyllocladia*, with the exception of *St. coralloides*, in which, as will be shown later, the coralloid form of the phyllocladia is secondarily derived.

Study of initial developmental stages in species of *Stereocaulon* shows, however, that the podetia may have another ontogenetic (and phylogenetic) mode of origin. In species possessing phyllocladia of squamulose form, the podetia are observed to arise by elongation of the *lower medullary tissue only* of the primary saxicolous phyllocladia, forming a naked, decorticate column without any assimilative layer of symbiotic algae. In Pl. II, Fig. 5 this type of development is shown in its initial stages in *St. botryosum*. The original primary phyllocladium, now raised up on the apex of the medullary stele, divides to produce secondary podetial phyllocladia of similar form, or in some instances simply enlarges to form a layer of cortex and assimilative algal tissue covering the upper side of the slantwise lengthening stele, this layer then subsequently breaking up into squamulose phyllocladia of the form characteristic of the species. This second type of development occurs in those species of *Stereocaulon* having phyllocladia of the verrucose, squamulose, crenate- or digitate-squamulose type, i.e, the so-called boreal species with which students of the genus in Europe and North America are familiar. It is represented in schematic form in Text-fig. 7 (p. 563).

Certain authors, such as Th. Fries (12, 13) and Galløe (14, 15) have considered the primary thallus of *Stereocaulon* to be hypothallus, reserving the term thallus for the podetia and phyllocladia. This view is incorrect, for as we have seen above, the primary thallus in this genus contains all the tissues which later go into the formation of the podetia, and is in fact a true thallus of the areolate- or squamulose-crustaceous type.

Vainio (48) demonstrated the thalline origin of the podetia in *Stereocaulon*, and called them *pseudopodetia*, to distinguish them from the true, carpogenically formed podetia of *Baeomyces*, *Cladonia*, etc. The accuracy of his observations being confirmed by the present study, it is proposed henceforth to make use of his term *pseudopodetia* with reference to the present genus.

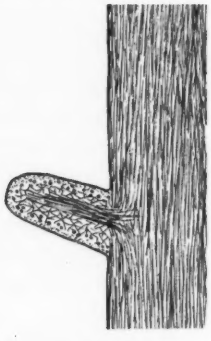
Origin and Development of the Phyllocladia

The phyllocladia of *Stereocaulon* are very characteristic of that genus. They are essentially assimilative bodies, and in the more highly developed species are the only part of the thallus (apart from the cephalodia) containing symbiotic algae and therefore capable of photosynthetic functions, being thus comparable to the leaves of the higher plants. Their increasing morphological complexity in some species, e.g. flattening to squamulose form, crenation, and palmate or digitate proliferation, might be explained as an adaptation tending to greater photosynthetic efficiency. They exhibit a considerable variety of form in different species, even within the same species, but these forms can be reduced to a limited number of fundamental types. Riddle (40) first distinguished in the boreal *Stereocaula* the following types of phyllocladium, for which he used the term "squamules": *palmate-digitate*, as in *St. paschale* and *St. tomentosum*; *coralloid*, as in *St. coralloides*; and *umbilicate to granular*, as in *St. denudatum*. Magnusson (27) amplified this classification, using the following terms: *coralloid*, as in *St. coralloides* and *St. subcoralloides*; *papillose*, as in *St. glareosum*; *verrucose*, as in *St. alpinum* and *St. incrustatum*; *granular*, as in *St. fastigiatum* (*botryosum*) and *St. spissum*; *squamuliform*, as in *St. Delisei*, *St. tomentosum*, and *St. coralloides* var. *occidentale*; *digitate*, as in *St. paschale*; *peltate*, as in *St. denudatum*; and *foliaceous*, as in *St. Wrightii* and *St. tyroliense*. Frey (10) repeats this classification without introducing any major modifications.

Phyllocladia of the truly coralloid branchlet-type are best studied in *St. ramulosum* (Pl. I, Fig. 1), in which they are very well developed and their origin easily detected. They are actually nothing but fine branchlets of the pseudopodetium, as has been proved by microtome sections, which show them to possess a central axial strand of parallel hyphae continuous with that of the pseudopodetium (Text-fig. 1).* In most species of this group they are notably *disharmonic*, i.e. considerably smaller than the pseudopodetial stem from which they abruptly spring; but in some species, and in some conditions of *St. ramulosum* itself, they tend to be quite or nearly *harmonic*, that is to say the terminations of pseudopodetial branches with a gradual decrease in thickness from the parent pseudopodetium, not showing any abrupt limit in their transition into the latter (Pl. III, Fig. 7, A). The term "disharmonic" is taken from a paper by Kajanus (22), in which he uses it to describe similar adventive branchlets in other lichens (*Ramalina*, *Roccella*). Frequently in *St. ramulosum* and other species with similar phyllocladioid branchlets it can be observed that those lower down on the pseudopodetium are harmonic, indistinguishable from normal small pseudopodetial branches, whilst those higher up are disharmonic, springing abruptly out of the much thicker pseudopodetial trunk.

* *Nägeli (29) shows on his Pl. VII, Figs. 10 and 11, sections very similar to our Text-fig. 1, but the species concerned are doubtful; said to have been* tomentosum, corallinum (*Syn.* coralloides) *and* alpinum (*Syn.* paschale *var.* alpinum).

For phyllocladia produced in this way, the term "phyllocladioid branchlets" (ramuli phyllocladioidei) introduced by Vainio (48) is descriptively correct, and is adhered to in the present study.



TEXT-FIG. 1. *Stereocaulon ramulosum* (Sw.) Räusch. Part of a longitudinal microtome section through a pseudopodetium and a disharmonic phyllocladioid branchlet, showing the continuation of the central axial tissue into the latter.

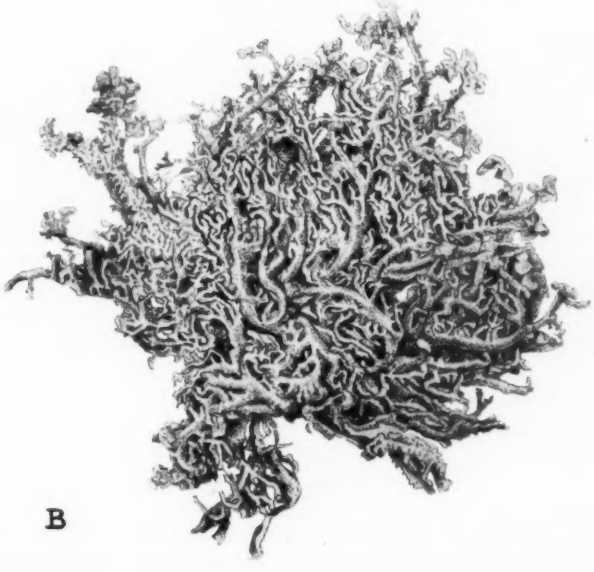
Development from the primary thallus has been observed in the following species of the group possessing terete-coralloid phyllocladioid branchlets:

St. caespitosum	*St. japonicum*
St. claviceps	*St. octomerellum*
St. curtatum	*St. prostratum*
St. gregarium	*St. ramulosum*

In *St. ramulosum* and *St. claviceps* the origin of the pseudopodetia by elongation and subsequent branching of the verrucose to coralloid phyllocladia of the primary thallus was observed (p. 525). In *St. curtatum*, *St. japonicum*, *St. octomerellum*, and *St. prostratum* the primary thallus likewise originally consists of verruculae which soon elongate in their entirety into coralloid-columnar form and then by enlargement and branching into pseudopodetia with phyllocladioid branchlets. In *St. caespitosum* and *St. gregarium*, as explained above, the primary thallus almost from the first consists of upright, coralloid or fingerlike structures, which become transformed into simple, corticate pseudopodetia merely by an increase in size, with little or no branching. They represent a persistently primitive condition of development in this group, not far removed from the hypothetical ancestral Toninioid form (see p. 575).

FIG. 7. A, *Stereocaulon ramulosum* var. *assimile* (Nyl. emend. M. Lamb) M. Lamb. The lectotype specimen from Bourbon Island in herb. Nylander (No. 40077 pr. p.), × 2.
B, *Stereocaulon Meyeri* var. *farinosum* (Th. Fr.) M. Lamb. The lectotype specimen from Mexico, Pico de Orizaba (Liebmann No. 74) in herb. Th. Fries, × 2.

A



B

True phyllocladia of the verrucose or squamulose type originate in quite a different manner. They are in fact the original squamules of the primary thallus, raised up on pseudopodetia, as described in the previous section (p. 526). For this reason, as might be expected, the primary thallus of *Stereocaula* of the group possessing squamulose phyllocladia is formed of sessile, saxicolous phyllocladia similar in form to those of the pseudopodetia (with one exception, *St. tyroliense;* see p. 564). This has been found to be the case in the following species of this group in which the primary thallus has been observed:

St. botryosum
St. condensatum
St. coralloides
St. evolutoides (var. *saxatile*)
St. glareosum
St. pileatum
St. supervestiens
St. tomentosum
St. vesuvianum

In all of these the pseudopodetia have been observed to originate as outgrowths of the basal medullary layer which, in the absence of a true hypothallus in *Stereocaulon*, fixes the primary phyllocladia to the substratum. This naked column carries up one or several phyllocladia on its summit, and as it elongates, its sides are colonized by additional phyllocladia of the same type. In *St. vesuvianum* (var. *umbonatum*) the pseudopodetial stalk may be produced downwards into a branched, rootlike structure penetrating into the crevices of the substratum. In *St. coralloides* the phyllocladia are distinctly terete-coralloid, and appear on outward inspection to be phyllocladioid branchlets of the *ramulosum*-type. In reality, however, they are not such, but are produced by secondary elongation into papillate and then coralloid form of true phyllocladia of the verrucose-squamulose type, as is well seen in some of its varieties, notably the var. *flabellatum*. In a Scottish specimen collected by the author a transition from flabellate-squamulose to terete-coralloid phyllocladia can be seen on the same pseudopodetium. Secondary papillate elongation of the phyllocladia occurs also in *St. glareosum*, *St. tomentosum* var. *myriocarpum*, *St. pileatum*, and *St. subcoralloides*.

Species of this group with true squamulose phyllocladia and pseudopodetia of medullary derivation may also produce phyllocladioid branchlets to a variable extent, these being merely the finest terminal pseudopodetial branchlets which retain a covering of more or less undifferentiated cortex. Occasionally these phyllocladioid branchlets may be more abundantly present than the true phyllocladia, as in *St. rivulorum* and often in *St. evolutum*. When they occur in *St. coralloides*, as for instance in the specimen distributed in Krypt. Exs. Vindob. No. 355, they could hardly be distinguished from the true, secondarily coralloid phyllocladia except by the fact that they lose their cortex and are sometimes terminated by apothecia.

In the exotic species *cornutum* and *flavireagens*, both belonging to the *vesuvianum*-group, a coralloid development of the phyllocladia has been occasionally observed. In *flavireagens* the coralloid structures occurred at the

base of the pseudopodetia, being apparently corticate adventitious branchlets of the latter and thus to be regarded not as true phyllocladia but as phyllocladioid branchlets. In *cornutum* the coralloid development was seen in the upper parts of the pseudopodetia, grading into the typical peltate-squamulose phyllocladia lower down, and was therefore an instance of secondary papillate-coralloid elongation of true phyllocladia as in *St. coralloides*.

True phyllocladia may be grouped in a series of increasing complexity in form. In some species they remain in a simple verrucose or grainlike condition, as in *St. Depreaultii* for instance, but in others they take on more elaborate and characteristic forms. Slight flattening and crenulation of the edges gives rise to phyllocladia of the *alpinum*-type; stronger flattening and more intense crenulation to the crenate-squamulose phyllocladia characteristic of *St. tomentosum*. If the crenulation becomes so marked as to form palmate- or digitate-squamulose structures, we have phyllocladia of the *paschale*-type, which are also found in *St. tomentosum* var. *myriocarpum*, and may in their extreme development take on a more or less coralloid form, as in *St. intermedium* and *St. sphaerophoroides*, in which they are sometimes hardly to be distinguished outwardly from phyllocladioid branchlets.

Phyllocladia of quite peculiar structure are found in the *vesuvianum* (*denudatum*) and *Wrightii* groups. They are characterized by darker (usually glaucous or olivaceous) central portions and lighter (whitish), often more or less raised and tumid margins. The darker centers consist of a hyaline, transparent, cortical layer, and the lighter margins of heavily inspersed-nubilated hyphal tissue. In the development of such a phyllocladium, the hyaline tissue is formed at a very early stage as a small lenticular inclusion above the gonidial layer. Phyllocladia of this type may be either lateral and peltate-squamulose, as in *St. vesuvianum* and allied species, or in the form of flattened, leaflike expansions on the ends of the pseudopodetia, as in *St. Wrightii*. A transition between these two types is seen in *St. confluens*. In the subspecies *santorinense* of *St. vesuvianum* only rudimentary pseudopodetia are developed, the plant consisting chiefly of a primary thallus of "denudatiform" phyllocladia, and the apothecia are developed, not on the pseudopodetia, but directly on the squamules of the primary thallus, a case of neoteny similar to that seen in *St. caespitosum* and *St. gregarium*.

Finally, mention should be made of a striking type of phyllocladium which occasionally occurs in exotic species, namely the lateral foliose type (not to be confused with the terminal foliose type represented by *St. Wrightii*). The classical example of this is the Himalayan *St. foliolosum*, in which the phyllocladia are leaflike and dorsiventral, but spring disharmonically out of the pseudopodetium like the phyllocladioid branchlets of *St. ramulosum*. Sections show them to be corticate on the upper side only, the lower side consisting of loosely intertexted hyphae; they are also seen to be provided with a central strand of chondroid hyphae continuous with that of the pseudopodetial axis, which proves that they are actually modified phyllocladioid branchlets. This is also confirmed by the structure of the cephalodia, which, as will be

demonstrated in the following section, is correlated with the exclusive development of phyllocladioid branchlets. In *St. foliolosum* var. *strictum* the phyllocladia in the lower parts of the pseudopodetia are of this foliose type, but those higher up are coralloid, and the gradual transition between the two types is then manifest. *St. virgatum* normally has terete, coralloid phyllocladioid branchlets, but occasionally (f. *applanatum*) some of them become flattened and leaflike as in *St. foliolosum*, and here again the gradual transition is seen. *St. cornutum*, a species of the *vesuvianum* group with true peltate-squamulose phyllocladia, often produces leaflike phyllocladia similar in appearance to those of *St. foliolosum*, but they are here derived by the transformation of true phyllocladia, and are not modified phyllocladioid branchlets.

Origin and Development of the Cephalodia

We are here concerned with the cephalodia of *Stereocaulon* with regard not so much to their often discussed physiological or functional significance as to their ontogenetic origin and their use as taxonomic criteria in the delimitation of species and groups of species within the genus. Their occurrence is characteristic of most species, and in many their presence seems to be quite constant; only in comparatively few *Stereocaula*, such as *St. scutelligerum*, *St. sphaerophoroides*, *St. virgatum*, and the "imperfect" species of the *quisquiliare–albicans* group, do they appear to be always lacking.

In the first half of the nineteenth century their nomenclature was vague and their taxonomic significance hardly considered. Th. Fries (12, 13) concreted their definition in the modern sense, although of course without recognizing their true nature; he distinguished the following two principal types in *Stereocaulon:* the brown-blackish, pulvinate type found in *St. paschale*, *St. denudatum*, etc., and the podicellate, subglobose, foveolate-scrobiculate type, more or less concolorous with the thallus, found in *St. ramulosum* and its allies. In his monographic descriptions of the individual species, he defined the outer form of the cephalodia tolerably accurately in each case as a secondary character, or in some instances, as in the *St. claviceps* group, as one of the characters separating natural stirpes of the genus.

Nylander, in his *Synopsis Lichenum* (32), diverted attention from the taxonomic significance of the morphology of the cephalodia, of which we find the first clear indications in the works of Th. Fries cited above, to the nature of the Cyanophyceous algae contained in them. He did not of course regard these as algae, even after the publication of Schwendener's researches on the dual nature of lichens in 1867 and 1868, but nevertheless was struck by their resemblance to the genera with which they are in fact identical, and used terms for them indicative of this resemblance ("stratum gonimon scytonemoideum", "sirosiphonoideum", etc.).* This concentration of taxonomic attention on the algal content of the cephalodia instead of on their morphology and structure has persisted almost to the present day, and has resulted in the description of several "species" separated on this character alone (e.g. *St.*

* *In a paper in Flora, 1866, p. 180, footnote, Nylander humorously coined the term "friesiades" for the algae in the cephalodia of* Stereocaulon.

arcticum, *St. Massartianum*, *St. mixtum*, *St. proximum*, the first mentioned published as late as 1938), in spite of the fact that Th. Fries already in 1866 and Forssell in 1883 had quoted instances of different forms occurring in cephalodia on the same plant, and even within the same cephalodium.

For a critical study of the cephalodia in *Stereocaulon* and their taxonomic significance we are indebted to a paper by Johnson (19) in which certain facts are established which allow the classification of the genus to be advanced on a reliable basis. Johnson concludes, as a result of comparative and statistical studies, that the gross morphology of the cephalodium is a good taxonomic character, three basic types being distinguished; that the cephalodia are organic and normal structures of the lichen, and not of pathological origin; and that the type of alga in the cephalodium has no taxonomic or phylogenetic significance. With a slight emendation of the last statement (see below), these main conclusions are supported by the studies of the present author.

The following three types of cephalodium are recognized by Johnson in *Stereocaulon*:

"*Spherical:* Cephalodia sessile or nearly so, at times partly immersed, often inconspicuous, hemispherical to subspherical, small, seldom over 1 mm. in diameter, the larger ones appearing in aggregates or irregularly rounded, gray to brown masses . . . ."

"*Botryose:* Cephalodia often stalked at maturity, similar in shape to bunches of grapes, concolorous with the podetium, cinereous to glaucescent, usually rather large, 2-4 mm. in diameter . . . ."

"*Scrobiculate:* Cephalodia usually stalked at maturity, globular but more or less clavate, pitted and furrowed with fine convolutions, concolorous with the podetium, whitish to ashy, often large and numerous, 1-7 mm. in diameter . . . ." (Johnson, op. cit., p. 738.)

These three types were found to show anatomical as well as morphological differences. The "spherical" type, as found in *St. tomentosum* and *St. paschale*, has a wall of loosely arranged, more or less peripherally (tangentially) running hyphae; the "botryose" type, studied in *St. exutum* and *St. japonicum*, is stated to be composed also of more or less loosely arranged hyphae, but in this case interwoven in various directions, not predominantly tangentially or vertically; and in the "scrobiculate" type, represented by *St. ramulosum* and *St. nesaeum*, the wall is formed of a closely packed tissue of radial hyphae.

The morphological difference between these three types of cephalodium is well shown by Satô's illustration (41, p. 51, Fig. 17).

The observations of the present author amplify these categories somewhat and seem to show that the limit between the "spherical" and the "botryose" types is not so definite as is suggested by Johnson.

In *St. tomentosum* the cephalodia are just as described above for the "spherical" type, being small, inconspicuous, not usually over 1 mm. in diameter, simple, and tumid or with only indistinctly lumpy or uneven surface, only rarely becoming more or less distinctly verruculose; often

appearing as mere aeruginose specks in the pseudopodetial tomentum. Similar primitive and undifferentiated cephalodia are also characteristic of *St. paschale* var. *alpinum*. In both these instances they contain nearly always *Nostoc*, rarely *Stigonema*. The other species quoted by Johnson as having "spherical" cephalodia is *St. paschale* (the typical species, as distinct from var. *alpinum*, which is often regarded as a separate species), but here the state of affairs is somewhat more complicated, as this species has been found to produce two distinct forms of cephalodia: those of the type described above (with *Nostoc*) occasionally occur, but usually they are different, being dark olive-brown, pulvinate to subglobose, with furfuraceous-scabrid to minutely tuberculate surface, as described by Magnusson (27, p. 47), and containing *Stigonema*. Most probably in this primitive type of cephalodium the color and form is conditioned by the alga present, and is hence without importance from a taxonomic point of view. In a specimen of *St. paschale* distributed in Arnold, Lich. Exs. no. 1363b (as "*Stereocaulon alpinum*"), both types of cephalodium were found in otherwise perfectly homogeneous material, and the same thing has been reported by Frey (10) in the type material of *St. paschale* f. *velutinum*.

Johnson describes and figures the formation of separate "capsules" of algae in cephalodia of the "spherical" type, with resultant division into chambers separated by hyphal walls (op. cit., p. 740, Pl. 67, Figs. 4-7). In the opinion of the present author it is but a small step from this condition to the "botryose" type of cephalodium, and indeed investigations which have been made in this respect suggest that no definite boundary exists between cephalodia of the "spherical" and "botryose" types, despite the very distinctive appearance of the extreme end forms.

The following data may be adduced in support of the foregoing statement. *St. tomentosum* vars. *myriocarpum* and *Orizabae* differ from the typical *St. tomentosum*, among other characters, in possessing larger and more complex cephalodia of a form not or hardly distinguishable from that designated as "botryose" by Johnson, their surface being usually distinctly divided into more or less discrete, botryform verruculae. Rarely, however, the var. *Orizabae* has been found to produce cephalodia of apparently simple, "spherical" structure, with more or less smooth and undivided surface. Sections through one of these apparently simple cephalodia revealed it however to be composed of a number of separate, compacted nodules, each containing a nest of *Nostoc*-algae enclosed in walls of compact, gelatinized hyphae; the general appearance being similar to that figured in Pl. 67, Figs. 6 and 7, of Johnson's paper, but in a more extreme form. It would seem therefore that the nature of the surface of the cephalodium, whether smooth or nodulose-tuberculate (botryose) is determined by the degree to which the nests or "capsules" of algae within the cephalodium multiply, and the completeness with which they become separated by walls of hyphal tissue.

Anatomically, according to Johnson, the "spherical" type differs from the "botryose" type in having the outer walls composed of more or less tangentially running hyphae, whereas in the latter the hyphae are intertexted

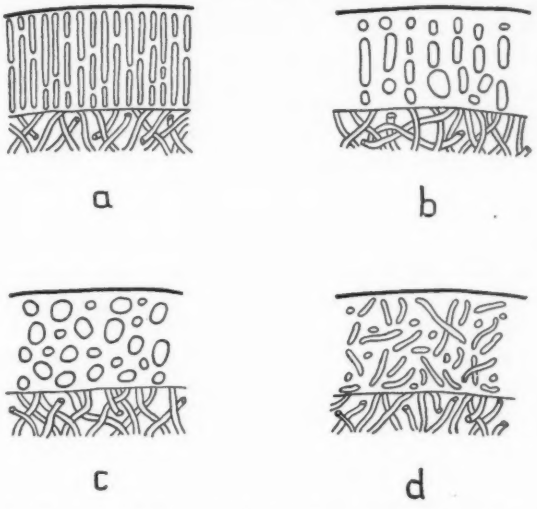
more at random in various directions. The present author has not been able to find any sharp division in this respect; in many cephalodia of simple undifferentiated form it appears that these are merely stages in the normal course of development, and in many instances it is hard to say whether the hyphae are running predominantly tangentially or are interwoven. In *St. tomentosum* var. *Orizabae*, referred to above, the cephalodia, whether botryose-verruculose (as is usually the case) or smooth, have a cortical layer of hyphae interwoven in various directions, at any rate at maturity.

Thus it is found that the "spherical" and "botryose" types of cephalodium distinguished by Johnson are connected by a series of imperceptible gradations, both morphologically and anatomically, and cannot in theory be maintained as distinct. The "botryose" type is however optimally developed in a number of species of the group possessing pseudopodetia of entirely corticate and assimilative origin, and phyllocladioid branchlets as the sole assimilative organs (*St. exutum*, *St. japonicum*, etc.), and the taxonomic section *Botryoideum* subsequently proposed by Johnson (20), with the synonymous section *Verruculata* of Satô (41), delimits, if emended in this sense, a natural series within this group, forming a sharp contrast to the series with foveolate-scrobiculate cephalodia (*St. ramulosum*, etc.). In these E. Asiatic species the "botryose" cephalodium is a very striking configuration, representing the highest development of the type, and the anatomy of the cephalodial wall has also advanced in complexity, having progressed from a structure of tangential or interwoven hyphae, as described by Johnson, to a distinctly paraplectenchymatic formation; this well seen in *St. exutum* (a specimen from Japan, Mt. Amagi, Asahina No. 104, examined), in which the wall is 12-20 μ thick, sordid yellowish-nubilated, and composed of more or less isodiametric, rounded or obtusely angular cells 3-4 μ in diameter, with walls 1 μ or somewhat less in thickness.

The cephalodia of the "scrobiculate" group are on the other hand sharply separated from the foregoing types, and undoubtedly represent, as demonstrated by Johnson on structural and statistical evidence, the most highly advanced type in the genus. This sharp distinction, together with the fact that they are practically constantly present in the species in which they occur, makes of them an excellent taxonomic criterion, for at this advanced stage they have attained a genetically conditioned fixity in form and anatomy which defies the modifying influence of external conditions and is independent of the nature of the algae which they enclose. The term "scrobiculate" or "foveolate-scrobiculate" (the latter originated by Th. Fries (12)) is perhaps better replaced by the designation "sacculate" (from *Stereocaulon* sect. *Sacculata* Satô (41)), since not all cephalodia of this type are scrobiculate-indented, but may be sometimes more or less smoothly spherical.

The important distinguishing character of the sacculate cephalodium is the structure of its cortex, which is always very well developed, thick and even, translucent and hyaline in section, and highly gelatinized, with the swollen walls of the hyphae entirely coalescent and indistinguishable; only the lumina of the hyphae are visible, appearing in section as tubes or rounded holes in a

homogeneous, transparent, mucilaginous matrix.* The shape and orientation of these hyphal lumina is subject to variation in different species or within the same species. In *St. ramulosum* they are constantly elongated, tubular, strictly parallel, forming a close palisade as shown on Pl. 68, Fig. 8 of Johnson's paper (op. cit., 1938) and in our Text-fig. 2, *a*. In some of the Asiatic species



TEXT-FIG. 2. Structure of the cortex in sacculate cephalodia. *a*, *Stereocaulon ramulosum* (Sw.) Räusch.; *b*, *St. nesaeum* Nyl.; *c*, *St. sorediiferum* Hue; *d*, *St. botryophorum* Müll. Arg.

of this group we find a gradual transition from this palisade arrangement to a paraplectenchymatic structure with isodiametric, rounded cell lumina. In *St. nesaeum*, for instance, most of the lumina are vertical (radial), parallel, and fistulose, but rounded and isodiametric cell cavities are often present among them, as shown in Text-fig. 2, *b*. *St. sorediiferum* often has all the lumina of the latter type (Text-fig. 2, *c*), the cephalodial cortex then presenting a quite paraplectenchymatic appearance, but within this same species transitional stages towards the palisade type can be found, many of the lumina being distinctly elongated. This intermediate condition can also be observed in *St. piluliferum* and some other allied species. *St. botryophorum* and *St. foliolosum* are peculiar in the complete lack of parallel orientation of the fused hyphae composing their cephalodial cortex, the lumina, mostly elongated and fistulose, being intricated in various directions (Text-fig. 2, *d*).

Cephalodia of the sacculate type are commonly scrobiculate-foveolate, i.e. with the surface irregularly wrinkled and furrowed, as in *St. ramulosum*,

** The structure of the cephalodial cortex should be examined in very thin freehand sections mounted directly in water; it has been found that most mounting media, especially syrups, affect the gelatinous tissue, altering the form of the lumina or making them indistinct.*

St. nesaeum, *St. sorediiferum*, etc. In the species of the *claviceps-macrocephalum* group, however, they are smoothly rounded and more or less globose, only rarely and at a late stage in their development becoming slightly indented. The scrobiculation and foveolation is due to the nature of the internal hyphal tissue, which in cephalodia of this type is always very lax and arachnoid, consisting of loosely entangled hyphae with considerable air spaces between them, and it is the lack of solidity of this internal tissue which brings about the partial collapse and folding of the outer wall. Most of the cephalodia of the smoothly rounded type, on the other hand, have a solid internal structure of compact hyphal tissue without air spaces. *St. piluliferum* is an exception to this rule, having the cephalodia lax and arachnoid internally, but it affords a transition to the *ramulosum–nesaeum* type, its older cephalodia becoming distinctly indented and foveolate. In most of the material seen to date of species with solid-cored sacculate cephalodia (*St. claviceps*, *St. macrocephalum*, etc.) the algal symbiont has been found to be *Nostoc*, whereas in species with loose-cored sacculate cephalodia (*St. ramulosum*, *St. nesaeum*, *St. sorediiferum*, etc.) *Stigonema* and *Scytonema* predominate. But that this is not always so is proved by an undescribed new species related to *St. nesaeum* and found in Indonesia, in which the cephalodia are solid-cored and contain *Scytonema*. In this instance the strongly growing *Scytonema*-filaments had brought about a limited disintegration of the compact, gelatinized, internal hyphal tissue of the cephalodium into discrete hyphae, but only in a few places, the greater part of the interior of the cephalodium remaining solid. This is of interest as showing that the solid-cored and the loose-cored cephalodia represent distinct natural anatomical types, and that the difference is not due merely to the algae which they contain.

A distinct modification of the sacculate type of cephalodium appears in the two known species of the *St. strictum* group (*St. strictum* Th. Fr., *syn. St. peladense* Vain., not *St. ramulosum* var. *strictum* Bab.). Here they are pale in color, more or less concolorous with the phyllocladioid branchlets, and of a branched-digitate or digitate-lobate form, in general appearance having a striking similarity to phyllocladioid branchlets (Text-fig. 3). In section they

TEXT-FIG. 3. Dactylaeform cephalodia of *Stereocaulon strictum* Th. Fr.

are found to be solid within, and provided with a hyaline, gelatinized cortex of the typical sacculate type with vertically (radially) parallel, fistulose cell lumina. A strand of chondroid central axis tissue runs into them from the pseudopodetium; the alga *Nostoc* in all the specimens seen. The form and

structure of these cephalodia strongly suggests that they may be derived by the modification of phyllocladioid branchlets (see below).

St. Colensoi, a New Zealand species, has cephalodia of a peculiar type, dissimilar to those found in any other known species, but at present it is not known with certainty whether it belongs to *Stereocaulon*, to *Pilophoron*, or to an undescribed genus, the statements with regard to its spores being conflicting. Its cephalodia are globose to club-shaped, finally becoming aeruginose-cinereous, large and conspicuous, borne on distinct pedicels. Their surface is not so much scrobiculate-foveolate as minutely granulate, but not verruculose or botryose. They are solid internally, connected with the core of the pseudopodetium by a continuation of the central axial strand, and have a thin, nubilated, paraplectenchymatic cortex of thin-walled, not gelatinized cells.

The Himalayan *St. botryophorum* has small, smoothly subglobose, sacculate cephalodia which frequently occur congregated together in masses of several, thus giving rise to a falsely botryose appearance. They may be termed compound-aggregate sacculate cephalodia.

The evolution of cephalodia of the "botryose" type from those of the simple, undifferentiated "spherical" type is easy to observe, and, as explained above, they grade into each other without sharp limits. The relationship of the highly developed sacculate type, with its very distinctive cortical structure, is more difficult to explain. Either it is developed in some way from the more primitive "spherical" or "botryose" types, or it has a completely different origin. Observations on the cephalodia of *St. implexum*, a member of the *St. ramulosum* group, produced evidence which seems to support the former alternative. This species has very typically scrobiculate cephalodia which in their optimal development become even more closely and finely foveolate-indented than in *St. ramulosum*. Usually they show the normal hyaline, gelatinized palisade cortex typical of the group, but in some specimens examined the younger cephalodia were found to possess a cortex like that of the "botryose" section, namely thin, sordid yellowish-nubilated, and paraplectenchymatic with thin-walled, more or less isodiametric cells. Older cephalodia on the same specimens were seen to develop, from the outside of this primary layer, a secondary cortex of the sacculate type by continued centrifugal growth, the transition between the two tissues being more or less gradual. Finally, as the secondary cortex increased in thickness, the primary nubilated layer was compressed and absorbed. In most individuals of *St. implexum* all the cephalodia, even the youngest ones, have only the typical hyaline, gelatinized, "sacculate" cortex, and it thus seems that the original "botryose" cortical layer has been almost entirely superseded in this group, persisting only as an atavistic feature in certain individuals. An interesting fact in this connection is that in a distinct, as yet undescribed, New Zealand variety of *St. implexum* all the cephalodia, even the oldest and strongly scrobiculated ones, were found to have a cortex of persistently "botryose"

structure, without development of the secondary gelified hyaline type. A similar transition has also been observed in the primitive species *St. corticatulum* (var. *subcorticatum*), in which the cephalodia have a variegated appearance, with darker (glaucous) patches alternating with lighter areas on their surface. The darker patches prove on sectioning to be cortex of the hyaline, "sacculate" type, while the intervening whitish tissue is nubilated cortex of the paraplectenchymatic "botryose" type.

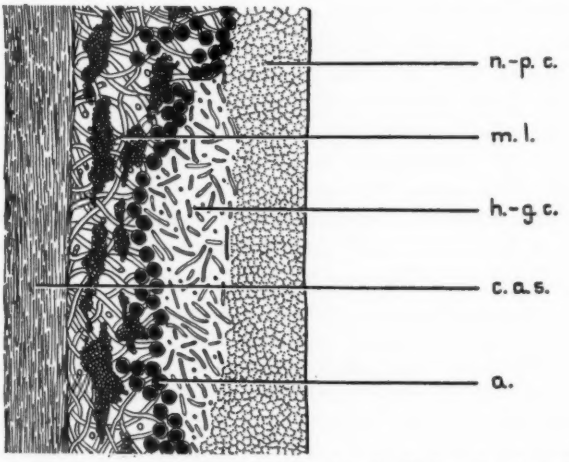
The important question now arises as to whether the cephalodia in *Stereocaulon* are of homologous origin in all species, and if so, whether they have been produced by the secondary modification of certain parts of the thallus. In undoubtedly primitive species with persistent primary thallus, such as *St. condensatum*, *St. caespitosum*, and *St. gregarium*, they occur basally on or between the phyllocladia, phyllocladioid branchlets, or developing pseudopodetia; in other species showing more complex development of the pseudopodetia they migrate upwards onto the sides of the latter. Since they are present and well developed in nearly all the undoubtedly primitive *Stereocaula* (with the exception of the "imperfect" *Stereocaula* of the *quisquiliare-albicans* group), it may with some certainty be assumed that they were acquired at a very early stage in the phylogenetic history of the genus, in all probability in the hypothetical ancestral crustaceous condition.

A study of the development of the cephalodia in undoubtedly primitive species may be expected to throw some light on their origin. Such a species is *St. caespitosum*, mentioned in the foregoing sections, and a morphological and anatomical study of the cephalodia in a syntype specimen yielded the following data.

In *St. caespitosum* the cephalodia are abundantly developed, being sessile at the base of the pseudopodetia, brown-blackish to black, irregularly pulvinate, becoming concrescent and more or less effuse, not botryose (as is stated in Redinger's original description) but with minutely scabrid surface as seen under a × 10 lens. In section they are solid internally, with nests of *Stigonema*-algae embedded at random in a compact, hyaline, hyphal tissue. Older cephalodia have no distinct cortex, the nodules of *Stigonema*-algae, with brownish sheaths, emerging to the surface; this is what gives rise to the minutely scabrid appearance which is seen macroscopically. Only in the youngest cephalodia is a distinct cortical layer developed, and it is found to be somewhat ill-defined, of variable thickness, and consisting of a hyaline, colorless, gelatinized tissue of completely fused, thick-walled hyphae confluent together into a clear mucilaginous matrix, in which the narrow, fistulose lumina, 1-2 μ wide, are seen running and anastomosing in various directions, in places also shorter, ellipsoid to rounded-cellular in section. This structure is similar to that found in the cephalodial cortex of *St. botryophorum* and *St. foliolosum* (Text-fig. 2, *d*, p. 535). Vertical sections show that a strand of pseudopodetial central axis runs into each cephalodium from the base, dividing into several divergent strands inside the cephalodium.

The presence of conducting pseudopodetial central axis tissue in the cephalodium does not necessarily indicate that the latter is of pseudopodetial origin, since conductive tissue of this type may be expected to be developed in any organ of photosynthetic function as a response to the need for transportation of the metabolic products. But the structure of the cortical layer as contrasted with that of the pseudopodetium or phyllocladioid branchlets is more likely to afford an indication of ontogenetic and phylogenetic relationship.

In *St. caespitosum*, as explained in a previous section, the pseudopodetia are merely enlarged primary digitate phyllocladioid branchlets. In section their cortical covering was found to be made up of two anatomically distinct types of tissue, viz.: in places the cortex consists of a yellowish-gray-nubilated, paraplectenchymatic tissue of thin-walled, more or less isodiametric cells 3-4 μ in diameter, persisting unchanged to the outer surface, and thus similar to the cortex of cephalodia of the "botryose" type in other species of *Stereocaulon*. In other places it is formed of a hyaline gelatinized tissue exactly similar to that described above in the cortex of the younger cephalodia. The resemblance between this latter type of pseudopodetial cortex and that of the cephalodia is so strong as to suggest forcibly the derivation of the latter by modification of pseudopodetia (or phyllocladioid branchlets). In the pseudopodetium of *St. caespitosum* the nubilated-paraplectenchymatic tissue is a centrifugal secondary outgrowth of the hyaline-gelatinized tissue, the



TEXT-FIG. 4. *Stereocaulon caespitosum* Redgr. Longitudinal section through part of a pseudopodetium, showing the two types of cortical tissue developed. *n.-p. c.*, nubilated-paraplectenchymatic cortex; *h.-g. c.*, hyaline-gelatinized cortex; *a*, algae; *m. l.*, medullary layer; *c. a. s.*, central axial strand.

latter representing the original primary cortex. This is seen from the fact that patches of the hyaline-gelatinized tissue occur beneath the nubilated-paraplectenchymatic tissue (Text-fig. 4), but not vice versa, and so we have

here a state of affairs the opposite of that observed above in the cephalodia of *St. implexum*, in which the development of the one type of tissue from the other is reversed.

If, as thus seems probable, cephalodia have originated by the modification of pseudopodetia or phyllocladioid branchlets, the dual anatomical nature of the pseudopodetial cortex noted in *St. caespitosum* may indicate the origin of the divergence between cephalodia of the "botryose" type and sacculate cephalodia. In *St. caespitosum* the cephalodia have adopted, perhaps fortuitously, the hyaline-gelatinized type of tissue for their cortical covering, and their further phylogenetic development would presumably be to the sacculate type, the morphological characters of which appear to be conditioned by the conglutinated, unyielding consistency of the cortex. The fact that they do not so develop in *St. caespitosum* itself is due to the feature that here the cortex soon becomes evanescent, and is hence incapable of impressing the morphological characteristics of the sacculate cephalodium. In the closely related *St. gregarium*, the cortex on the cephalodia is persistent, and is also of the hyaline-gelatinized sacculate type; the cephalodia are typically sacculate, becoming distinctly rugose-scrobiculate in the later stages of their development. Cephalodia clothed with the second, nubilated-paraplectenchymatic type of pseudopodetial cortex might be expected to develop into the "botryose" type, and do indeed appear to have done so in the case of *St. curtum* (Räs.), a Patagonian species obviously derived from the *caespitosum–gregarium*-complex. Both these types would equally represent modifications of the pseudopodetium, or of phyllocladioid branchlets, or, if we consider the development of cephalodia to have taken place already prior to the acquisition of the fruticulose orthotropic growth form, of the bullae or squamules of the ancestral crustaceous thallus. Perhaps also in some instances both types of tissue might be taken up in the cortex of the cephalodium, one or other of them finally developing more vigorously and suppressing the other; this would explain the transition between the two types observed in cephalodia of some individuals of *St. implexum* (p. 537).

The hypothesis that the cephalodia of *Stereocaulon* are modified pseudopodetia, phyllocladioid branchlets, or phyllocladial squamules admittedly rests on somewhat slender evidence at present, but no observed facts have yet been found to conflict with it, and the obvious similarity of the cephalodia to the phyllocladioid branchlets in the *St. strictum* group, mentioned above, strongly supports it. In more primitive, crustaceous genera with development of cephalodia, such as *Placopsis* (Lecanoraceae), the latter arise as independent microthalli which are later surrounded by and raised up upon the other microthalli with Protococcoid symbionts; the two types of microthalli being of identical origin (soredial hyphae or spores), and their development into cephalodia or thallus-areolae depending apparently on their first random association with Cyanophyceous or Protococcoid algae respectively. See the researches of Sernander, mentioned in Lamb (24, p. 158).

Johnson (19) has shown that a general statistical correlation exists between the evolution of the cephalodia and increasing complexity of spore form in *Stereocaulon*. In general terms, his results are as follows (op. cit., p. 745):

"*Cephalodia lacking:* The apothecia also are often lacking." This certainly holds good for the "imperfect" *Stereocaula* of the *quisquiliare-albicans-arbuscula* group. The single fertile species used to illustrate this section, *St. pygmaeum* Vain., must be ruled out, because it is not a *Stereocaulon*, but synonymous with *Lecania* (*Thamnolecania*) *Brialmontii* (Vain.) Zahlbr. (see Lamb (26, p. 236)). We may add to this section the species *St. scutelligerum*, *St. sphaerophoroides*, and *St. virgatum*, which appear to be constantly destitute of cephalodia.* Their spores are 3- (rarely 4- or 5-) septate, and between 30 and 56 μ in length, which accords more or less satisfactorily with Johnson's scheme, although it must be pointed out that as regards vegetative characters they appear to be species of a high order of evolutionary development.

"*Spherical:* spores 20-39 μ in length, 3-7-septate." The list of 13 species (or 12 omitting *St. sphaerophoroides*, which does not appear to belong here) illustrates this correlation well. The spore data for *St. Wrightii* may be added from the descriptions of Savicz (42) and Asahina (3): 3-5-septate, 12-23 μ in length.

"*Botryose:* spores 24-100 μ in length, 3-16-septate." The list of 10 species given needs some emendation, which reduces the suggested correlation considerably. *St. botryophorum* and *St. foliolosum*, the two species with the longest and most septate spores, do not belong to this section, but have sacculate cephalodia, according to the present author's examination of the type specimens. The remaining species all have spores not over 7-septate and not over 55 μ in length, and so it is seen that the distinction between the cephalodia of the "spherical" and the "botryose" types, which we found to be a vague one morphologically and anatomically, is also not supported to any great extent by correlated spore features.

"*Scrobiculate:* spores 35-200 μ in length, 3-29-septate." 13 species listed. The correlation in some of the species, notably *chlorocarpoides*, *macrocephalum*, *nesaeum*, *piluliferum*, *sinense*, and *soredii ferum*, is striking; but *St. ramulosum* (syn. *St. mixtum* and *St. proximum*, and including *St. macrocarpum*, which is not specifically distinct) has spores of a relatively primitive type, not over 7-septate and not over 60 (-70) μ in length. However, Johnson's study clearly shows a general correlation of the advanced sacculate type of cephalodium with a highly developed spore form. It is also of interest to note that the most advanced species in these respects all seem to have their center of distribution in the Himalayan region (see p. 568).

* *Tuckerman described "scrobiculate-foveolate" cephalodia in the type of his* St. maderense, *which is synonymous with* St. sphaerophoroides, *but in the type specimen of the former the present author could find no trace of cephalodia. Johnson (op. cit., p. 746) attributes cephalodia of the "spherical" type to this species. The author has never succeeded in finding cephalodia in* St. sphaerophoroides, *although a large material has been examined.*

The peculiar lobed-digitate cephalodia of the *St. strictum* group, described above, appear on the same correlative grounds to represent a highly evolved type, as the spores in these species are long and multiseptate (more so than is indicated in Johnson's table).

Another table in Johnson's paper (op. cit., p. 748-9) shows the correlation between the form of the cephalodia and that of the phyllocladia. Species with "spherical" cephalodia are seen to have generally verrucose to squamulose or palmate-digitate or peltate phyllocladia, i.e., true phyllocladia representing the squamules of the primary thallus, the only species in the section with "coralline" phyllocladia being *St. coralloides*. As we have seen above, this exception is only an apparent one, for in that species they are not actually phyllocladioid branchlets as appears on first sight, but secondarily elongated true phyllocladia. Genuinely coralloid phyllocladioid branchlets as the sole assimilative organs seem to make their appearance first in the section with botryose cephalodia, and a group of species combining these characters has its center of distribution in Japan (*St. japonicum*, *St. curtatum*, *St. exutum*, etc.). In the species with sacculate cephalodia the assimilative organs are seen without exception to be phyllocladioid branchlets, and this is a rather remarkable fact which obviously has a distinct bearing on the classification of the genus. The only species in which the correlation is not perfectly clear is *St. botryophorum* (wrongly placed in Johnson's table), in which the phyllocladioid branchlets are of a somewhat indeterminate form, apparently a secondary reduction from the coralloid branchlet type.

Johnson's investigations and those of the present author on the correlation between cephalodial and phyllocladial types allow the following general statements to be made:

1. Simple, primitive cephalodia without distinct botryose division are associated with true phyllocladia of the verrucose, squamulose, squamulose-digitate, palmate, or peltate types borne on pseudopodetia of medullary origin.

2. Cephalodia of the "botryose" type, a more complex but not essentially different development of the foregoing type, are associated with either true phyllocladia on pseudopodetia of medullary origin or phyllocladioid branchlets on pseudopodetia derived by the elongation of all the tissues of the primary thallus.

3. Cephalodia of the sacculate type are constantly associated with phyllocladioid branchlets borne on pseudopodetia derived by the elongation of all the tissues of the primary thallus.

A final word with regard to the occurrence of different algal types in cephalodia of the same species. There appears to exist in certain cases a distinct preference for one particular type of Cyanophyceous alga, capable of expression as a statistical percentage if enough material is available for examination, and perhaps in some species reaching 100% constancy. Thus

the Japanese species with phyllocladioid branchlets and botryose cephalodia (*japonicum*, *curtatum*, *exutum*, etc.) almost always have *Stigonema* in the cephalodia. *St. ramulosum* and its f. *elegans*, of which sufficient material has been seen to allow a statistical comparison in this respect, show a marked difference in their selection of cephalodial algae; the typical species usually containing *Stigonema* or *Scytonema* in the cephalodia, only rarely (in about 15% of the cases) *Nostoc* or *Gloeocapsa*. The f. *elegans*, on the other hand, which is distinguishable morphologically and has a distinct distributional area, has the cephalodial algae in approximately the following proportions of frequency: *Nostoc*, 80%; *Gloeocapsa*, 12.5%; *Stigonema*, 7.5% and *Scytonema*, 1.5%. This may of course be a result of differences in availability of distinct algal types in different areas, and not an indication of active selection on the part of the lichen, but until further statistical and perhaps also experimental evidence comes to hand, the possibility of a certain degree of correlation of the cephalodial algae with morphological and taxonomic characters may not be dismissed entirely. To distinguish species or forms on this basis alone, however, is certainly an unjustifiable procedure.

Apothecia and Pycnidia

The majority of species of *Stereocaulon* produce apothecia abundantly and fairly constantly, and their outward form, internal structure, size and septation of spores, etc. is a useful and important feature for the classification, in some respects superior to the vegetative characters, which are subject to considerable variation through the influence of diverse ecological and climatic conditions. In some species, notably the so-called "imperfect" *Stereocaula* of the *quisquiliare–albicans–arbuscula* group, apothecia have never been recorded with certainty, and perhaps never occur. These species also lack cephalodia, and therefore their inclusion in the genus *Stereocaulon* can only be a provisional one, subject to revision if apothecia are eventually found and may prove to belong to a different morphological or sporological type.

The apothecia of *Stereocaulon* may be either lateral on the pseudopodetia or pseudopodetial branches (sometimes on short pedicels) or terminal on their ends. They vary greatly in size in different species, being commonly smaller when lateral and larger when terminal. Very small apothecia are usually characteristic of the *vesuvianum* (*denudatum*) group, and also of *St. tomentosum* and most of its varieties. The largest known in the genus are found in *St. intermedium* and *St. Saviczii*, in which they are up to 6 or 7 mm. in diameter, and they may become almost as large in some states of *St. ramulosum*.

In some of the species with long multiseptate spores (*St. claviceps*, *St. piluliferum*, etc.) the pseudopodetium immediately below the developing apothecia is swollen into clavate or barrel-shaped form; these swellings appear in the earliest stages of apothecium formation, the disk first becoming visible as a punctiform indentation in their apex. At this stage the developing fruit bodies somewhat resemble those of *Sphaerophorus*. In fully mature apothecia the swelling becomes reduced, finally often hardly noticeable, but

in those which have not reached their full development it is often very conspicuous, especially in *St. claviceps*. "Hypophysis" seems a suitable term to employ for these formations.

For a long time it was considered that apothecia of both lecideine and lecanorine type occurred in *Stereocaulon*, and a division into two subgenera, *Lecidocaulon* and *Lecanocaulon*, was made on this basis (Zahlbruckner (51, 52)). This division is based on faulty observation, and has no natural foundation; in reality, only apothecia of the lecideine, biatorine, or superlecideine* type occur in *Stereocaulon*, and if in some cases sporadic groups of gonidial algae are found in the lower parts of the central cone or on the outer margin of the amphithecium, they are of secondary occurrence, having penetrated subsequently upwards from the subtending pseudopodetial tissues. In some species, e.g. *St. scutelligerum* and *St. pityrizans*, a conspicuous, light colored, pseudothalline margin (amphithecium) is present at least in the younger stages, being an extension of the pseudopodetial cortex, and gives the apothecia a quite lecanoroid appearance, but on sectioning it is found to be destitute of symbiotic algae internally. The subgenus *Lecanocaulon* therefore does not exist in reality (see p. 559).**

The apothecia are bounded by a proper margin (parathecium or amphithecium), which often becomes reflexed and excluded at maturity. In most species it has a characteristic palisade structure, being formed of radiating, conglutinated, highly gelatinized and very thick-walled hyphae; in a few species, as in the *tomentosum* group, it may be reduced or more or less indistinct, with the hyphae not exclusively in parallel palisade arrangement. In many species it can be observed to merge into the pseudopodetial cortex without any sharp limit, thus confirming its amphithecial nature.

Most of the species of *Stereocaulon* in which apothecia are known show an internal medullary layer, or central cone, inside the apothecia below the hypothecium. This central cone often grades imperceptibly into the upper part of the pseudopodetial central axis, and like the amphithecium, is of vegetative (pseudopodetial) origin, formed by the intrusion of medullary hyphae into the base of the apothecium. It may be of lax texture, with discrete and rather loosely entangled hyphae, as in *St. ramulosum*, or compact and completely gelatinized, with the hyphae fused into a mucilaginous matrix in which only their fistulose, interlacing lumina are visible; as in the species of the *St. paschale* and *tomentosum* groups. Often it contains scattered or confluent aggregations of opaque, more or less granular substance (either calcium oxalate or depsidone lichen acid); this has been found to be a variable

* *In superlecideine (or "superlecideoid") apothecia an amphithecium of thalline cortical tissue, without symbiotic algae, is present on the outside of the apothecium (Frey (11)).*

** *This fact was clearly recognized by Th. Fries, who writes in Lichenogr. Scandin. I (1871) p. 43: "Apothecia . . . primum haud raro lecanorina . . . . apparent et excipulo thallode instructa . . . Qualia autem apothecia si microscopio examinamus, excipulum extus videmus omnino ejusdem esse naturae ac stratum thalli exterius, gonidiis modo destitutum."*

feature of no taxonomic significance. The hyphae composing it are colorless, with one exception, *St. curtum* (Räs.), in which the upper part of the central cone tissue is sordid yellowish- to brown-pigmented.

In most of the species of the *vesuvianum* (*denudatum*) group the central cone is usually much reduced, indistinct, or evanescent, the apothecia here closely approaching the simple protolecideine condition, and their proper margin apparently not of amphithecial origin but a true excipulum, probably formed by the sterilization of thecial elements.*

The hypothecium varies from colorless (or grayish- to sordid yellowish-cloudy) to pigmented (various shades of brown). This character of unpigmented versus pigmented hypothecium is important for the classification, but only up to a certain point; it serves to distinguish species or varieties, but not higher categories. For this reason the segregation by Vainio of a special section *Phaeobasis* on the grounds of the pigmented hypothecium is unjustified (see p. 560). Occasionally the hypothecium may be so strongly nubilated with a dull brownish, minutely granular substance that it appears in section to be pigmented, but on application of potassium hydroxide to the section the nubilation is dissolved, and the tissue then seen to be in reality unpigmented. The transition between the hypothecium and the central cone may be gradual or abrupt. An abrupt transition is seen in *St. implexum* and *St. tennesseense*, in both of which the hypothecium is colorless, hyaline, and translucent, contrasting sharply with the underlying, heavily yellowish-gray-nubilated, more or less opaque central cone tissue. This character has been found to be constant in *St. implexum*, and very serviceable for the identification of that species.

The thecium (hymenium) shows variation in height within the genus, and as the height is fairly constant within each species, it is a useful taxonomic criterion. A low thecium (40-70 μ) is found in species belonging to the *paschale*, *tomentosum*, and *vesuvianum* (*denudatum*) groups; only the exotic species possess a high thecium, the most marked in this respect being those with elongated, multiseptate spores (*nesaeum*, *claviceps*, and *piluliferum* groups), in which the thecium may attain a height of 180 μ. The paraphyses are always discrete under pressure in water, never gelatinously conglutinated, and vary in thickness from 1 to 2 μ; when thick, they are more or less straight, but when thin are often sinuose and filiform. Their heads are nearly always distinctly capitate or clavate-capitate (up to 3-5 μ) and more or less brown-pigmented; brown is the only epithecial color known to occur in *Stereocaulon*, and this indicates a sharp separation from the genus *Pilophoron*, in which the epithecium is of an aeruginose-blackish color. Occasionally fine granules are present in the upper part of the thecium. The asci are variously clavate,

* *Reinke (39) figures a section through an apothecium of* St. denudatum (*Fig. 49, II*) *which does not correspond to reality, for the margin of the apothecium is represented as a continuation of the pseudopodetial central axis. On the basis of this faulty observation, Reinke was led to the erroneous conclusion that in* Stereocaulon *the pseudopodetium is a continuation of the foot of the apothecium, i.e. a true podetium.*

elongate- to cylindric-clavate in some species, shortly and broadly clavate in others, and their wall is commonly thin at the sides (about 1 μ) and gelatinously thickened at the apex (up to 7 or sometimes 12 μ).

The spores of *Stereocaulon* are, by the definition of the genus, colorless, elongated, and variously transversely septate; as a rule only young immature spores are found completely lacking in septa. Their size and the number of septa in them varies considerably, and shows a phylogenetic development from the more simple to the more complex forms, as has been pointed out by Johnson (19). In a few species, such as *St. lavicola* (emend.), they may be predominantly or even exclusively 1-septate, with a single median septum, but in most they are 3- or more septate. There appears to exist a natural division between species with the spores up to 7-septate and species with the spores more than 7-septate. On the basis of the sporological characters, the most highly evolved species of *Stereocaulon* appear to have their center of distribution in Asia, chiefly in the Himalayan region, where we find such species as *St. macrocephalum* and *St. sinense*, in which the maximal degree of evolution in this respect is reached, the spores being vermiform, sinuous, up to 150 or even 200 μ in length, and with as many as 30 septa. When the spores are thus long and vermiform, they are often too long to be fully extended inside the ascus, and are then packed in a close spiral or corkscrew-like formation. In a few species of low sporological evolution, such as *St. paschale*, the spore septa may sometimes be poorly differentiated and indistinct, presumably by secondary degeneration.

Very little is known concerning the carpogonic development in this genus, the only species which have been yet investigated cytologically in this respect being *St. paschale* (Wolff (50)) and *St. coralloides* (M. & Mme. Moreau (28)). In the former, Wolff could find no trichogynes or female organs, the development of the apothecia seeming to take place in a purely apogamous manner, in spite of the presence of pycnidia. In *St. coralloides*, the Moreaus found ascogonic coils consisting of uninucleate hyphae, and in some instances at least these were provided with a trichogyne reaching to the surface, but there degenerating, without any fertilization by pycnoconidia having taken place. The cells of the ascogenous hyphae become binucleate at a relatively late stage in the formation of the apothecium, the actual method of diploidization not having been observed; structures similar to the clamp connections of Basidiomycetes were found on the diploid ascogenous hyphae, which seems to indicate that the binucleate condition originates in some apogamous manner (e.g. by cell fusions) lower down in the ascogenous mycelium. Sexual reproduction is therefore at present unknown in *Stereocaulon*, and if this state of affairs should prove to be general, it will be a fact of some taxonomic consequence, for as apomictic populations the species will naturally lack certain features of evolution shown by interbreeding groups.

Frey (10) has distinguished four basic types of apothecial structure in the European *Stereocaula*, naming them "tyroliense-Typus", "alpinum-Typus",

"tomentosum-Typus", and "paschale-Typus" respectively. The extra-European *Stereocaula* show also other and widely different features of apothecial anatomy. Not having made a special study of the apothecia of *St. tyroliense*, the present author cannot offer any opinion as to its qualifications as a distinct anatomical type, but from investigations made on *St. paschale*, its var. *alpinum*, *St. tomentosum*, and other related species, he considers that the "alpinum-", "tomentosum-", and "paschale-" types of Frey belong together and represent merely different developmental stages of the same fundamental structure. The apothecia of *St. tomentosum* represent the simple, juvenile stage of this development, and appear by their small size to be arrested in this condition. The proper margin is poorly differentiated, and it is hard to say whether it is of amphithecial or parathecial origin; the central axis of the pseudopodetium remains undivided at the point of insertion into the apothecium, its hyphae becoming gradually converted into those of the central cone, which is either solid, without air spaces or cavities, as represented in Frey's sketch (op. cit., p. 73, Fig. 10, 3) or may be ruptured into several large air cavities in its lower part by the division of the pseudopodetial central axis inside the apothecium; in the latter case the appearance in section is similar to that figured by Frey, loc. cit., Fig. 10, 4, for his "paschale-Typus", except that the apothecium remains plane and with broader attachment to the pseudopodetium. In the species of this type with large apothecia (*St. paschale* and its var. *alpinum*, for instance) the younger apothecia correspond in structure to the "tomentosum-Typus" described above, but as they grow larger with age the proper margin, which is here distinctly recognizable as an amphithecium, originally continuous below with the cortex of the pseudopodetium, becomes torn away from the latter by the lateral expansion of the apothecium, and remains only at the margins; the underside of the apothecium is then formed by the now exposed central cone tissue. At the same time the branching of the upper end of the pseudopodetial central axis becomes more marked, until finally the pseudopodetium, at its point of insertion into the apothecium, is divided into a number of fine corymbose branchlets, each with its separate point of insertion into the underside of the apothecium. *St. paschale* var. *alpinum* usually does not show this advanced stage of development, but in a specimen from South Georgia with unusually large apothecia, about 2.5 mm. in diameter, it was found to be well shown. The typical *St. paschale* usually exhibits marked rupture of the central cone tissue by branching of the pseudopodetial axis inside the apothecium, but seldom has the pseudopodetium branched externally, outside the apothecium. The final development of this type is seen in *St. paschale* var. *grande*, in which the large terminal apothecia are supported on the underside by a bundle of conspicuously corymbose, small pseudopodetial branchlets, and the rupturing of the inner tissues of the apothecium by the divergence of the pseudopodetial axis strands proceeds so far that finally the apothecium becomes completely divided into several smaller secondary apothecia. The same development is seen in some of the extra-European species, such as *St. intermedium*. This type, in its

various stages of development, may be called the "paschale-type", and includes, as mentioned above, the groups distinguished by Frey as "alpinum-Typus" and "tomentosum-Typus".

The apothecia of the *St. vesuvianum* (*denudatum*) group, with few exceptions, may be considered to form a type of their own, characterized by minute size, poor differentiation or complete absence of central cone tissue, margin of parathecial origin, shallow hypothecium, and the frequent occurrence of brown or brownish pigmentation in the various tissues (margin, central cone, and hypothecium). They are similar in structure to the simple protolecideine apothecia of crustaceous genera, such as *Lecidea*, *Catillaria*, *Bacidia*, and *Toninia*, and are undoubtedly primitive.

In the more highly evolved species of exotic *Stereocaula* the central cone becomes strongly developed, filling up a large part of the interior of the apothecium. In some of these exotic species it is compact in texture, with the hyphae gelatinously fused, as in *St. virgatum*, *St. sorediiferum*, etc., in others it is lax, with interstices between the hyphae, as in *St. ramulosum* and allied species.

Pycnidia have been observed in about 40 species of *Stereocaulon*. They usually occur at or near the apices of the pseudopodetia, often immediately below the apothecia, and are globose structures provided with a brown or brownish, more or less paraplectenchymatic wall which often has internal extensions dividing the interior of the pycnidium into several labyrinthiform compartments. The fulcra, so far as known, are of the exobasidial type. The pycnoconidia in some species, e.g. *St. paschale*, have been found to show considerable variation in size, but in other species they appear to be more or less invariable, and therefore useful as a confirmatory character in identification. They vary in form and size within the genus from shortly bacillar, about 4 μ long and 0.7-1.0 μ broad, to filiform and more or less arcuate, conmonly 8-12 μ long and about 0.5 μ broad. The latter type is found in some of the species of the *vesuvianum* (*denudatum*) group, and in the species with phyllocladioid branchlets and sacculate cephalodia (*St. ramulosum*, *St. Meyeri*, *St. nesaeum*, *St. pilophoroides*, *St. sinense*, *St. sorediiferum*, etc.). In *St. platycladum*, a distinct species of the *vesuvianum*-group, the pycnoconidia are 16-24 μ long, the longest known in the genus.

Soredia

Apart from spores, soredia are the only other type of diaspore found in *Stereocaulon*. They are known in about 23 species. In some, such as *paschale* and *evolutoides* they are very rare and probably atypical or accidental; in others, such as *Delisei*, *leprocephalum*, *pileatum*, and *tyroliense*, they are constant and characteristic of the species.

According to the classification of soredia introduced by Du Rietz (8), the soredia in *Stereocaulon* may be either of the diffuse or of the limited type. Quite diffuse soredia, derived from the deliquescence of the phyllocladial

cortex over large areas, are met with in *St. botryosum* (var. *dissolutum*). In the probably accidental sorediate states of *St. paschale* and *St. evolutoides* they are intermediate between the diffuse and the limited type, forming more or less separate pulvinate excrescences, which however flow into each other without sharp limit. In fact, most of the sorediate species of *Stereocaulon* produce soredia which cannot be placed exclusively in either of the main categories of Du Rietz (diffuse and limited); the commonest form being an apical, capitiform soredium which covers the apex of the podetium but also spreads downwards for some distance and merges imperceptibly into the phyllocladial or cortical covering of the pseudopodetium (Pl. III, Fig. 7, B). Well limited soredia of the apical capitiform type are found in *St. leprocephalum* and *St. pileatum*.

The soredia are usually farinose, consisting of very small diaspore particles, but may be granulose, formed of comparatively coarse grains; the latter type in *Stereocaulon* has been found to be derived directly from phyllocladia by a gradual diminution in their size, as for example in *St. botryosum* var. *dissolutum* and *St. violascens*, in which the granulose soredia are actually very reduced phyllocladial granules, showing all stages of transition into normal phyllocladia. In soredia of the farinose type, no transition into phyllocladia is to be observed, the diaspore particles being formed by direct breaking up of the cortex of the pseudopodetia or phyllocladia. In some species, e.g. *capitellatum* and *farinaceum*, the soredia take on the function not only of propagation but also of assimilation, replacing the phyllocladia almost entirely as photosynthetic organs.

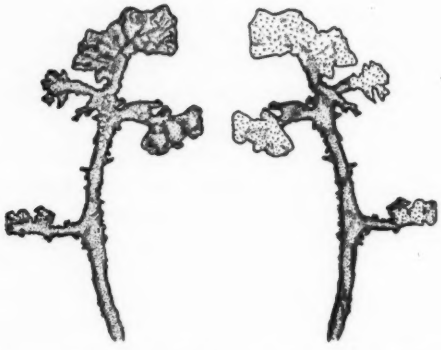
In *St. Delisei*, a species possessing apical soredia, the pseudopodetium often finally divides into a number of very fine branchlets inside the soralium.

A few species produce soredia on one face of flattened, leaflike or spathulate expansions. In *St. botryosum* var. *spathuliferum* and *St. explanatum* (*nom. nov.*, see p. 582), these bifacial expansions are formed by the flattening of the ends of the pseudopodetia. In *St. tyroliense* they are the upright squamules of the primary thallus. These expansions are corticate on the upper side, decorticate and sorediate on the lower. Text-fig. 5 shows their appearance in *St. explanatum*, as seen from both upper and lower sides.

Apical soredia in *Stereocaulon* usually occur on the ends of the pseudopodetia themselves, but occasionally are found on the ends of the phyllocladioid branchlets (in *St. sorediiferum* and *St. strictum*). In this case they are very small, and are not constantly produced.

The "imperfect" *Stereocaula*, *albicans*, *arbuscula*, *quisquiliare*, and *tenellum*, can hardly be said to possess true phyllocladia. In these species the function of assimilation is carried on by minute sorediiform granules which in outward appearance and anatomical structure can scarcely be distinguished from soredia. Whether they really are such is doubtful, for they are firmly attached to the pseudopodetium and do not appear to function as detachable diaspores as do the loosely adnate granules of true soredia.

The presence of soredia in *Stereocaulon* cannot be regarded as a character of great taxonomic significance, as they occur indiscriminately in species of obviously diverse affinity. They afford a good distinguishing character in certain species in which their occurrence is constant, but in other species their production is variable, and in some, as pointed out above, they are almost certainly abnormal or accidental.



TEXT-FIG. 5. *Stereocaulon explanatum* M. Lamb (Syn. *St proximum* var. *compressum* Nyl.), from Bolivia, near Unduavi, coll. Eyerdam, 1939 (No. 26073). Terminal bifacial sorediate expansions of the pseudopodetia, showing dorsal and ventral surfaces. × 2·5.

Chemical Constituents and Their Taxonomic Significance

Biochemical research and its application to taxonomy has probably made greater progress in the lichens than in any other group of plants, mainly owing to the investigations of Zopf, Asahina, Seshadri, and others. The empirical discovery of chemical reactions with potassium hydroxide and calcium hypochlorite was announced by Nylander in 1867 (33). Although some contemporary workers, notably Müller Argoviensis,* flatly rejected chemical methods as having no place in classification, their value soon came to be generally recognized, and present day lichenologists, with a few exceptions, consistently employ them as an important character in the description of species.

In most of the taxonomic literature where chemical reactions are mentioned, no attempt is made to identify the actual substance causing the reaction. Zopf, in his classical book on the chemical compounds of lichens (53), analyzed and named many of them. Asahina, who possesses the unique advantage of being both biochemist and taxonomic lichenologist, has taken the chemical study of lichens further and has originated, firstly the useful Paraphenylenediamine test, and secondly a microchemical method whereby lichen acids can

* *"Wo zwei Flechten einzig und allein durch die Reaction verschieden sind, wo also alle übrigen structurellen und äusseren Charaktere harmoniren, da muss ich energisch gegen eine specifische Trennung protestiren und betrachte alle so fabricirten Arten als Null und Nichts" (Müller Arg. in Flora, LXXIV, p. 385, 1891, criticizing Wainio's "Etude sur la Classification naturelle et la Morphologie des Lichens du Brésil").*

be identified by the form of the crystals which they produce when treated with various solutions under the microscope. This microchemical method has the great advantage of requiring only a small fragment of the lichen for testing, thereby avoiding the risk of contamination inherent in the macrochemical analysis of a large bulk of material.

With the use of the long established potassium hydroxide and calcium hypochlorite reactions alone, it is seldom possible to arrive at an exact determination of the substance causing the reaction. Paraphenylenediamine used in conjunction with potassium hydroxide, however, will in many instances permit of an identification (see the table given by Asahina (2, p. 50)). In cases where reactions alone are insufficient to differentiate between distinct lichen acids, recourse must be had to the microchemical method mentioned above.

It is obviously desirable, whenever possible, to mention in the description of a species, not only its reactions, but also its exact chemical constitution. This has been done by Asahina in his taxonomical publications, but most other lichenologists, not being trained in biochemistry, remain content with stating the reactions only.

The possibilities of chemical investigation as an aid to taxonomy are now becoming more and more strongly realized also by the phanerogamic botanists, and it has been found that many of the larger subdivisions of flowering plants, such as families, sections, and genera, originally delimited on a purely morphological basis, are characterized also by biochemical differences; see a paper on the subject by Gibbs (16).* The application of chemical methods in the phanerogams, however, does not yet seem to have reached the point at which species are distinguished on chemical characters. This is a problem with which the phanerogamic botanists will find themselves faced sooner or later, and their method of dealing with it will be awaited with interest. One instance quoted in recent literature is that of an Australian tree, *Leptospermum citratium*, of which different specimens were found to contain different essential oils (Penfold, Morrison, and Smith-White (34)). The authors' solution was to regard the chemically different plants as "variety A" and "variety B" of the species, and their approach is therefore different from that of the lichenologists, most of whom would regard such a chemical difference as constituting a distinct species. Degelius (5), considering this problem as it affects lichenology, asks: "Weshalb soll man in der Flechtensystematik ganz andere Grundsätze befolgen als bei anderen Pflanzengruppen?", and goes on to say: "In keiner anderen Pflanzengruppe schreibt man Merkmalen solcher Art grössere systematische Bedeutung zu . . . Wenn morphologisch dieselben Typen vorliegen und nur chemische Unterschiede bestehen, handelt

* *Chemical characters have also been enlisted in systematic zoology, notably in the study of the Lepidoptera, in which Ford (Proc. Roy. Entomol. Soc. London, Ser. A. XVI (1941) 65), has found instances of chemical differences corroborating taxonomic divisions made on a morphological basis, or suggesting new groupings the validity of which was subsequently confirmed by a revision of the morphological characters.*

es sich meiner Ansicht nach höchstens um verschiedene Rassen derselben Art. Die Systematik muss sich jedoch in erster Linie auf die Morphologie stützen, nicht auf die Chemie."

At present lichenologists are separated into two distinct schools of thought in their approach to this problem. The first group, represented by Asahina and the specialists on *Cladonia*, ascribe specific importance to chemical differences alone; the second, like Degelius quoted above, refuse to do so unless there are morphological characters also present to support the chemical ones. Some lichenologists simply ignore the chemical characters, and omit to mention the reactions in their diagnoses.

The problem would be less complicated if the lichens were simple organisms, but they are not, and it is not exactly known to what extent the formation of the characteristic lichen acids depends on the symbiotic union of the fungal and algal components. Probably most of the reactive compounds are produced by the fungus alone, and in some instances this has been proved experimentally; thus Thomas (44) proved that the fungal components of *Caloplaca elegans* and *C. murorum* were able to form the yellow substance parietin also in pure culture, without the aid of the symbiotic algae, and the same capacity has been found by Castle & Kubsch* to be manifested by the fungal component of *Cladonia cristatella*, which produces usnic, didymic, and rhodocladonic acids in cultural isolation from its algal partner. It is to be expected, however, that the nature of the alga present must often influence the production of chemical compounds by the fungus, and it has been plausibly suggested by Asahina (4) that the two morphologically similar but chemically and algologically different *Lobaria* species, *L. pulmonaria* and *L. retigera*, the former with protococcoid algae, the latter with *Nostoc*, have the same fungal component, modified in its physiological characteristics by the metabolic difference due to the distinct algal symbionts; "Da die verschiedenen Gonidien verschiedene Assimilationsprodukte liefern würden, so ist es kein Wunder, dass ein und derselbe Pilz verschiedene Stoffwechselprodukte zu produzierten im stande ist, falls die Gonidien verschieden sind" (Asahina, op. cit., p. 762). If this hypothesis corresponds to the facts, as seems very probable, the logical conclusion must be that in such a case as this *the chemical difference cannot be considered as a taxonomic character of the lichen*, because the latter must be regarded and classified as a fungus living in symbiosis with algae, the taxonomic treatment referring to the fungus alone, and not to the alga (which already has its own separate classification as a distinct subdivision of the plant kingdom), nor to the lichen body as a whole regarded as an indivisible combination, the latter being a mystical concept which cannot be upheld on scientific grounds. It would appear obvious that a taxonomic epithet can apply to one single organism only, and not to a combination of two, but this appears to have been overlooked by some lichenologists. It is true that the lichen exhibits certain characters possessed by neither of its components separately, and that the algae have entered into such an intimate union with

* *In Arch. Biochem. 23 : 158. 1949.*

the fungal component that they might be compared with the chloroplasts of the higher plants; also that the whole somatic organization of the lichens, in distinction to that of the fungi, is conditioned by the need for photosynthetic efficiency on account of the presence of chlorophyll in the symbionts, as has been emphasized by Reinke (39); but these arguments cannot alter the fact that the lichen is a fungus living in symbiosis with an alga, no matter how intimate may be the connection between the two, and that it must be classified accordingly, i.e. as a fungus. See the remarks of Nannfeldt (31) and Nannenga (30) in this respect.

Instances like that of *Lobaria pulmonaria* and *L. retigera* quoted above, in which the only noticeable difference is in the algal symbiont or the chemical constitution, the fungal component being presumably the same, are quite common in the lichens, especially in the genus *Cladonia*, and are not lacking in the genus *Stereocaulon* which is dealt with in the present paper. Two instances may be quoted. *St. Wrightii* Tuck. and *St. apocalypticum* Nyl. are identical in outward appearance and have been regarded in the literature as synonymous; but the former contains atranorine and stictic acid, giving the reaction paraphenylenediamine + orange-red, while the latter contains atranorine and lobaric acid, with faintly yellowish to negative paraphenylenediamine reaction. *St. tomentosum* contains stictic acid (paraphenylenediamine + red); the E. Asiatic plant described by Zahlbruckner as "*Stereocaulon Sasakii*" is morphologically indistinguishable from *St. tomentosum*, but contains lobaric acid (paraphenylenediamine + faintly yellowish or −). With the "imperfect" *Stereocaula* of the *albicans–arbuscula* group the matter becomes more complicated, for here we may find as many as five chemically different types quite indistinguishable from each other morphologically, and separable only by the use of reagents or by microchemical analysis.

Not only may distinct chemical substances be produced by outwardly indistinguishable individuals, but the content of the same lichen acid may fluctuate in individuals of the same chemical constitution, owing to the influence of environmental and geographical factors, as has been demonstrated by the present author in the genus *Neuropogon* (Lamb (25)), so that a negative chemical reaction in a species normally giving a positive reaction cannot be regarded as taxonomically significant, and should be registered merely as indicating an inactive "phase" of the species.

In the author's taxonomic revision of *Stereocaulon*, an attempt was first made to follow the traditional method of separating "chemical species", but so many instances of the type described above were found, especially in the so-called "imperfect" *Stereocaula*, that to follow out the system logically would have necessitated the description of about 40 "new species" on chemical characters alone, a procedure which in the opinion of the author would have little to recommend it, especially since some of these "species" could be distinguished only by microchemical tests which most working lichenologists appear to have neither the time nor the inclination to carry out. This solution

of the problem having been rejected as unsatisfactory and probably unscientific, it was nevertheless realized that the chemical characters noted could not be simply ignored, for in many species they appear to be quite constant, and therefore a valuable aid to identification; and also in certain at least of the species manifesting two or more distinct chemical types, the latter undoubtedly possess an important regional or phytogeographic significance, as in *St. tomentosum* and "*St. Sasakii*" mentioned above. Obviously it is necessary to register chemical differences where they occur, but this should preferably be done outside the framework of formal taxonomy, in order to avoid burdening the literature with a mass of new epithets which most probably lack a sound scientific basis.

With these considerations in mind, the author has elaborated the following method of dealing with the "chemical species" in the hope that it may be considered and judged on its merits by other taxonomic lichenologists.*

It is suggested that morphologically indistinguishable lichen individuals which contain distinct lichen acids should be regarded as belonging to one and the same species, and that the chemical difference should be expressed by the use of the term "strain" (Germ. "Stamm", Fr. "Lignée", Sp. "Linaje") with the Roman numerals I, II, III, etc., the number I always standing for the typical strain, that is, the strain in which the actual type specimen of the species occurs; the nature of the chemical compound present being added in brackets (if necessary with a query mark if not identified with certainty by analytical tests), together with the specific or subspecific epithet (in quotation marks) by which the strain in question is represented or has been formerly designated, provided that such an epithet already exists.

The following examples will make the application of the method clear.

Stereocaulon Wrightii Tuckerm., Ch. str. I (Stictic acid or typical strain).
" " Ch. str. II (Lobaric acid or "apocalypticum"-strain).

Stereocaulon tomentosum Fr., Ch. str. I (Stictic acid or typical strain).
" " Ch. str. II (Lobaric acid or "Sasakii"-strain).

Stereocaulon arbuscula Nyl., Ch. str. I (Squamatic acid or typical strain).
" " Ch. str. II (Fumarprotocetraric acid or "aberrans"-strain).
" " Ch. str. III (Physodic acid strain).

Stereocaulon albicans Th. Fr. emend. M. Lamb, Ch. str. I (typical strain, of undetermined chemical constitution).
" " Ch. str. II (Atranorine or "gracilescens"-strain).
" " Ch. str. III (Stictic acid ? or "subgracilescens"-strain).

* *This proposal was presented at the International Botanical Congress in Stockholm in 1950 on behalf of the author by Dr. Eilif Dahl, and is now to be considered by the nomenclatorial commission. It has also been put forward by the author in a letter appearing in Nature, 168:38. 1951.*

Cladonia chlorophaea (Flk.) Spreng.,* Ch. str. I (Fumarprotocetraric acid or typical strain).
" " Ch. str. II (Grayaninic acid or "Grayi"-strain).
" " Ch. str. III (Cryptochlorophaeic acid or "cryptochlorophaea"-strain).
" " Ch. str. IV (Merochlorophaeic acid or "merochlorophaea"-strain).
" " Ch. str. V (Novochlorophaeic acid strain).
" " Ch. str. VI (Usnic acid strain).
" " Acid-free phase.

Hypogymnia furfuracea (L.) Krog,* Ch. str. I (Physodic acid or typical strain).
" " Ch. str. II (Olivetoric acid or "olivetorina"-strain).

It remains to be seen whether the above solution will prove a satisfactory one. If not, and if the method of distinguishing the chemical strains as distinct species should after all prove to be the correct one, the system has the advantage of allowing the change to be made, merely by giving them taxonomic epithets if none have previously existed, together with a short Latin diagnosis to validate them. In any case, lists of species in floristic publications should always register the chemical nature of the individuals cited by one or other of these methods, because, as mentioned above, the chemical differences may often be significant from a phytogeographical point of view.

The lichen acids were until recently considered to be peculiar to lichens, but it has since been demonstrated by Raistrick, Robinson, and Todd (36) that physcion (parietin), the orange-yellow emodin monomethyl ether characteristic of the Caloplacaceae and Teloschistaceae, is produced also by an *Aspergillus* of the *glaucus* series. They are, as pointed out by Seshadri (43), apparently built on an altogether original pattern. Various theories have been advanced to explain their significance, but the truth probably is that they are nothing more than excretion products, as has been suggested by Quispel (35). Those which furnish the characteristic reactions with potassium hydroxide and paraphenylenediamine belong to the groups known as Depsides and Depsidones, which are orcine derivatives of the aromatic series. The following is a list of the chemical compounds at present known to occur in the genus *Stereocaulon*:

1. *Depsides*

Atranorine, $C_{19}H_{18}O_8$. Found occurring alone in *St. albicans* (Ch. str. II), *St. condensatum*,** *St. curtatum*, *St. implexum*, *St. incrustatum*, *St. ramulosum* (Ch. str. I), and an undescribed Japanese species. It is also found as an accessory constituent in most of the species containing stictic acid, lobaric acid, and dendroidin.

* *Example communicated by E. Dahl in litt., 30. xi. 1950.*
** *According to Zopf (53).*

Baeomycetic acid, $C_{19}H_{18}O_8$. Found in an undescribed Peruvian species.

Divaricatic acid, $C_{21}H_{24}O_7$. Found (in conjunction with psoromic acid) in the Ch. str. III of *St. pseudoarbuscula*.

Squamatic acid, $C_{19}H_{20}O_9$. Found in *St. arbuscula* (Ch. str. I).

Thamnolic acid, $C_{19}H_{16}O_{11}$. Found in *St. arbuscula* (Ch. str. III).

Lecanoric acid, $C_{16}H_{14}O_7$. Found in Ch. str. VII of *St. pseudoarbuscula*. The only known occurrence in *Stereocaulon* of a compound giving a red reaction with $CaCl_2O_2$.

2. *Depsidones*

Stictic acid, $C_{19}H_{14}O_9$. Found (usually in conjunction with Atranorine) in *St. claviceps*, *St. coralloides*, *St. japonicum* (Ch. str. I), *St. Meyeri* (Ch. str. II), *St. nesaeum* (Ch. str. II), *St. tomentosum* (Ch. str. I), *St. vesuvianum*, incl. *denudatum* (Ch. str. I), also other species of the *vesuvianum* group, *St. Wrightii* (Ch. str. I), *St. Argus* (ch. str. II), and two undescribed Japanese species.*

Lobaric acid, $C_{25}H_{28}O_8$. Found (usually in conjunction with Atranorine) in *St. exutum*, *St. intermedium*, *St. japonicum* (Ch. str. II), *St. octomerellum*, *St. octomerum* (Ch. str. I), *St. paschale*, *St. pileatum*, *St. prostratum*, *St. sorediiferum*, *St. tomentosum* (Ch. str. II), *St. Wrightii* (Ch. str. II), and three undescribed Japanese species.

Salazic acid, $C_{18}H_{12}O_{10}$, *Salazic acid α-methyl ether*, $C_{19}H_{14}O_{10}$, and *Norstictic acid*, $C_{18}H_{12}O_9$.* These three compounds all give a yellow then red KHO reaction, with formation of acicular crystals under the microscope. One or other of them is found in *St. flavireagens*, *St. lavicola* (emend.), *St. Maunae-Loae*, *St. nesaeum* (Ch. str. I, norstictic acid proved), *St. ramulosum* (Ch. str. III, norstictic acid proved), *St. scutelligerum* (norstictic acid proved), and *St. virgatum*.

Fumarprotocetraric acid, $C_{22}H_{16}O_{12}$. Found in *St. arbuscula* (Ch. str. II) and probably in the Ch. str. IV of *St. pseudoarbuscula*.

* *According to Asahina (in J. Japan. Botany, XIV, p. 655. 1938), the stictic acid contained in* Stereocaulon *species usually has some admixture of norstictic acid.*

Psoromic acid, $C_{18}H_{14}O_8$. Found (in conjunction with divaricatic acid) in Ch. str. III of *St. pseudoarbuscula.*

Physodic acid, $C_{26}H_{30}O_8$. Found in *St. arbuscula* (Ch. str. IV).

3. *Diphenyleneoxide derivatives*

Dendroidin, $C_{16}H_{12}O_8$. Found (in conjunction with atranorine) in *St. octomerum* (Ch. str. II), *St. pendulum*, *St. strictum* var. *lecanoreum*, and *St. vesuvianum* var. *umbonatum* (Ch. str. III). As no data on this newly discovered lichen compound have yet been published, the remarks on it by Prof. Asahina *in litt.* are here quoted: "It is a colourless needles of m. p. 293°. The alcoholic solution is coloured bluish green by ferric chloride and dark bluish green by $Ca(OCl)_2$. The acetone extract . . . yields on recrystallization from G. E. solution under cover glass colourless ± curved needles. The formula corresponds to $C_{16}H_{12}O_8$ and seems to belong to a diphenyleneoxide derivative (just as Strepsilin and didymic acid)."

4. *Cumarones*

Usnic acid, $C_{18}H_{16}O_7$. Found in *St. quisquiliare* (Syn. *St. nanum*, *St. microscopicum*).

5. *Compounds of the fatty series*

Various undetermined fatty acids found as accessory constituents in *St. albicans* (Ch. str. II) and several strains of *St. pseudoarbuscula.*

6. *Of unknown composition*

An unidentified and as yet unnamed lichen acid found in *St. tenellum.* Asahina writes *in litt.*: "Acetone extract of tenellum is coloured by $FeCl_3$ in alcoholic solution beautifully bluish green. Moistened with KHO coloured brownish then wine red." The paraphenylenediamine reaction on the thallus is + (quickly) salmon-pink.

Finally, a few hints on the practical use of reagents in *Stereocaulon* may be given. Formerly the reactions were usually made on the pseudopodetia in this genus, either on their surface or on the cut open central axis; *St. coralloides* and *St. subcoralloides*, for instance, are distinguished in the literature by this method. It has been found, however, that tests on the pseudopodetia, external and internal, are unreliable, and this is not surprising when it is considered that these are more or less woody conducting structures removed from the centers of active assimilation and metabolism (the phyllocladia or phyllocladioid branchlets). In other plants, such as shrubs and trees, we

should select the leaves and growing points for biochemical investigation rather than the lignified trunks. The potassium hydroxide and paraphenylenediamine reactions in *Stereocaulon* should therefore be studied on the phyllocladia or phyllocladioid branchlets, and not on the pseudopodetia. If soredia are present, the reagents should be applied to them also, for they are rich in metabolic substances and give more distinct reactions even than the phyllocladia. The chemical reactions in *Stereocaulon* are more subtle and less conspicuous than in e.g. *Cladonia*, and must be carried out with care and attention under a lens or binocular microscope. Those obtained with paraphenylenediamine are usually not instantaneous; species containing stictic acid, for example, often take up to half a minute to develop the full orange-red coloration with paraphenylenediamine. Those which contain atranorine, either alone or in conjunction with lobaric acid, give within the space of about half a minute a very faint sulphur-yellow coloration with paraphenylenediamine. If no reaction occurs within about one minute, the result may be classed as negative, for any subsequent color change will be a spurious one produced by the oxidation of the paraphenylenediamine solution. Some species vary considerably in the concentration of lichen acid which they contain, and may give negative reactions on the phyllocladia, but positive reactions are often then revealed in sections of the apothecia treated with the reagents under the microscope; as for instance in *St. nesaeum* and *St. virgatum*.

The microchemical tests of Asahina are described in the following of his publications, under the title "Mikrochemischer Nachweis der Flechtenstoffe": J. Japan. Botany, XII (1936) 516, 859, XIII (1937) 529, 855, XIV (1938), 39, 244, 318, 650, 767, XV (1939) 465, XVI (1940) 185.

Taxonomic Subdivision of the Genus

Dodge (7) has dealt with the typification of the genus *Stereocaulon*, and gives the following information. The name was originated as a section of the old genus *Lichen* by Schreber in 1791; he did not cite any species belonging to it, and hence the typification encounters difficulties at the outset. It was raised to generic rank first by Schrader in 1794, but applied by him to the genus *Pertusaria* (*P. corallina*). Strictly speaking therefore the type species of *Stereocaulon* is *Pertusaria corallina*, and the name *Stereocaulon* would have to be used in place of *Pertusaria*, which was not published until 1805. If this were done, then the old generic name *Coralloides* (Dill.) Hoffm. would have to be used for *Stereocaulon*. As a genus, *Stereocaulon* was first used in the present accepted sense by Hoffmann in 1796, although he included in it also species belonging to other genera, viz., *Sphaerophorus*, *Pertusaria*, *Lichina*, and *Parmeliella*. The true *Stereocaulon* species cited by him are *St. quisquiliare*, *St. condensatum*, and *St. paschale*. It seems from the data given as if neither *Stereocaulon* nor *Pertusaria* could be upheld in their present sense if the rules of nomenclature were rigorously applied, and it is obviously desirable to place both of them on the list of *nomina conservanda*. Dodge selects *St. paschale* as the type of the genus, this species having been mentioned under

Stereocaulon (either as a proper genus or as a subgenus of *Lichen*) by both Acharius (1794, 1798) and Hoffmann (1796). Assuming that the name will be conserved, it seems best, pending the clarification of the International Rules of Botanical Nomenclature on this point, to cite the genus as *Stereocaulon* (Schreb.) Hoffm., not (Schreb.) Schrad.

Several attempts have been made from time to time to divide *Stereocaulon* into natural subgenera or sections, but most of these have proved more or less arbitrary and unnatural.

Körber, in his Syst. Lich. German. (1855), divided the genus into two sections, *Cereolus*, "minora, thallo simpliciusculo, protothallo persistente", including *St. condensatum*, *St. cereolinum* (=*St. pileatum*), and *St. nanum* (=*St. quisquiliare*), and *Eustereocaulon*, "maiora, thallo repetito-ramoso, protothallo subevanescente", including all the other central European species.

Th. Fries, in his De Stereoc. et Pilophor. Comment. (1857), took up Körber's section *Eustereocaulon*, subdividing it into two groups, *Saxifraga* and *Terrestria*, according as to whether the pseudopodetia are firmly attached at the base or emorient and loosely attached. As a second section be proposed *Chondrocaulon*, to accommodate the single species *St. nanum* (*St. quisquiliare*).

Nylander, in Bull. Soc. Bot. France, XXV (1878) 352, proposed to include *St. nanum* (*quisquiliare*) in a proper genus of its own, *Leprocaulon*, also including here subsequently *St. arbuscula* (Lich. Insul. Guineens. (1889) 8). In Synops. Lich. (1860) 232, he suggested that *St. Colensoi* should constitute "fere genus proprium", *Corynophoron*, and in Lich. Nov. Zeland. (1888) 15, made the formal combination under that genus. Also in Synops. Lich., on p. 233, he segregated a group of species with supposed lecanorine apothecia under the heading: "fere genus proprium: LECANOCAULON".

Tuckerman, in his Genera Lichenum (1872), created a subgenus *Phyllocaulon* for *St. Wrightii*, which differs from the other species in having, in place of lateral squamulose phyllocladia, foliose apical expansions of the pseudopodetia.

Vainio, in his Etud. Lich. Brésil (1890), proposed to divide the genus into two subgenera, *Lecidocaulon* Vain., with lecideine apothecia devoid of symbiotic algae, and *Lecanocaulon* (Nyl.) Vain. (based on Nylander's "fere genus proprium" of 1860), with the apothecia supposed to be lecanorine and containing symbiotic algae. This classification has been taken up by Zahlbruckner in Engler & Prantl's Nat. Pflanzenfam. and in Cat. Lich. Univ., but is one of the least satisfactory subdivisions of the genus, being completely erroneous, since no truly lecanorine apothecia are known to occur in *Stereocaulon* (see p. 544). In a subsequent paper (Ann. Acad. Sci. Fennic., Ser. A, VI, No. 7 (1915) 25), Vainio partially corrected this error by substituting for the old subgenus *Lecanocaulon* three new sections, *Phaeobasis* (with brown hypothecium), *Diplocheilon* (with a pseudothalline or supposedly thalline margin on the outside of the excipulum), and *Myelocarpon* (with a lax central cone having interstices between the hyphae). But these divisions also have been

found by the present author to be unnatural and of little taxonomic value, especially the section *Phaeobasis*, which, as has already been pointed out by Redinger (38), separates such closely related species as *St. caespitosum* and *St. gregarium*, and unites together such discrepant elements as *St. cornutum* and *St. salazinum* (=*scutelligerum*).

Riddle, in Botan. Gaz. L (1910) 285, takes up Körber's section *Eustereocaulon* and Th. Fries' section *Chondrocaulon*, and adds another, *Prostereocaulon* Riddle, for the species with persistent primary thallus (*St. pileatum* and *St. condensatum*), i.e. corresponding to Körber's section *Cereolus*, which he rejects on nomenclatural grounds.

Du Rietz, in a short paper on the Scandinavian *Stereocaula* published in Svensk Bot. Tidskr. XX (1926) 95, introduces a suggestive classification in which use is made also of the form of the phyllocladia. There are two main subsections, *Macrocarpa* DR. with apothecia mostly terminal and large, and *Microcarpa* DR. with apothecia mostly lateral and small. The subsection *Macrocarpa* is again divided into two series, *Cylindrophylla* DR. with cylindrical-coralloid phyllocladia, and *Squamophylla* DR. with squamulose or verrucose phyllocladia.

Dodge, in his *Synopsis of Stereocaulon* (Ann. Cryptog. Exot. II (1929) 93), follows Riddle in distinguishing the sections *Prostereocaulon* and *Chondrocaulon*, and adds to these the section *Stereocladium* (based on the genus of that name published by Nylander in Flora, LVIII (1875) 302) for *St. tyroliense* and some other species. The rest of the species listed by Dodge are not placed under any subgeneric or sectional name.

Satô, in Nakai and Honda's *Nova Flora Japonica* (1941), pages 57 and 82, proposed to separate as distinct sections the species with botryose cephalodia (as sect. *Verruculata* Satô) and those with sacculate, scrobiculate-corrugated cephalodia (as sect. *Sacculata* Satô). The same suggestion with regard to the botryose species was made independently and almost simultaneously by Johnson, who published the new section *Botryoideum*, founded on the same type species (*St. exutum*) as Satô's sect. *Verruculata* (Johnson in Bryologist, XLIV (1941) 7).*

Clements and Shear, in *The Genera of Fungi* (1931), pages 127 and 320, distribute the species of *Stereocaulon* among three separate genera, "*Stereocaulum*", "*Lachnocaulum*", and "*Chlorocaulum*". "*Stereocaulum*" comprises species with a proper excipulum and spores with several cells, and is founded on *St. paschale*; "*Lachnocaulum*" (apparently a distorted version of *Lecanocaulon*) includes species supposed to have a thalline margin to the apothecia and simple spores, and is based on *St. Colensoi* (in which, by the way, the nature of the spores is disputed); and "*Chlorocaulum*" is intended to accommodate the species with supposedly thalline margin to the apothecia and spores with several cells, *St. salazinum* (=*scutelligerum*) being quoted as the type species.

* *Johnson's publication appeared in February 1941, and Satô's in May 1941, so that* Botryoideum *as a section has priority over* Verruculata.

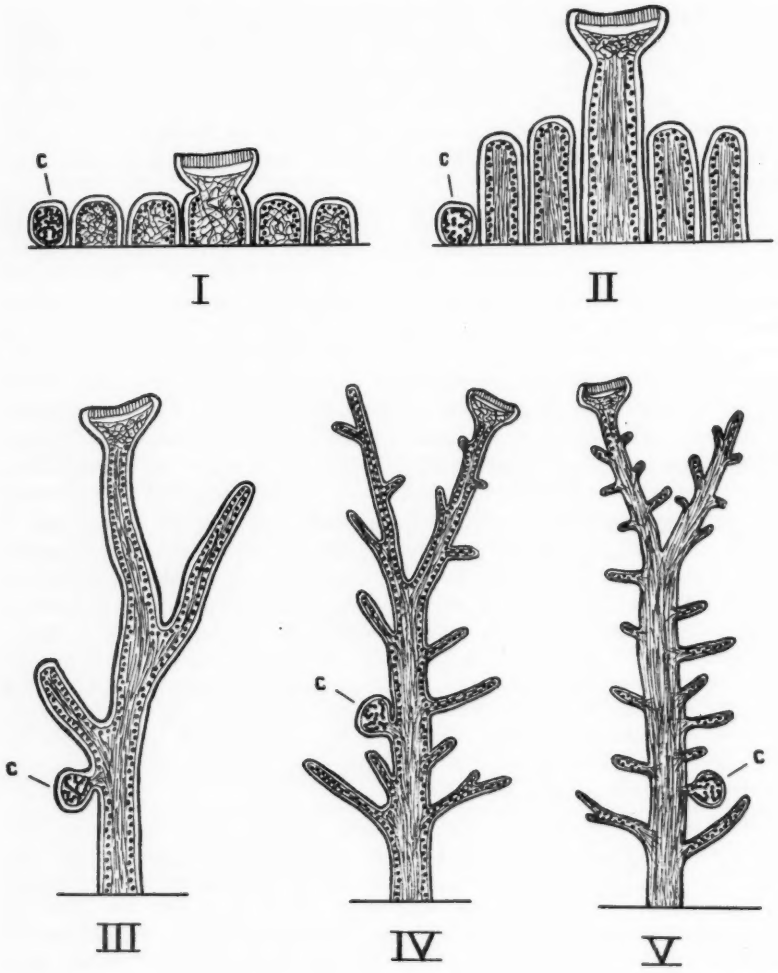
Apart from the orthographic errors perpetrated, this "classification" demonstrates the pitfalls awaiting authors who attempt on the basis of literature alone to make taxonomic divisions in groups with which they are not familiar.

Finally, Räsänen, in his *System der Flechten* (Acta Bot. Fennica, XXXIII (1943) 10), enumerates the following five sections of *Stereocaulon*: *Diplocheilon* Vain., *Lecidocaulon* Vain., *Myelocarpon* Vain., *Phaeobasis* Vain., and *Phyllocaulon* (Tuckerm.) Räs.

Some of the foregoing subdivisions are natural ones and deserve a place in an emended subgeneric classification of *Stereocaulon*, while others, as shown above, are worthless. The suggestion of Du Rietz (loc. cit.) regarding the natural distinction between species with coralloid phyllocladia (phyllocladioid branchlets) and those with squamulose or verrucose phyllocladia appears to be a sound one, for as we have seen on p. 528 of the present paper, these two types have a distinct ontogenetic origin. Tuckerman's *Phyllocaulon*, based on *St. Wrightii*, is also a good natural subdivision, although transitions from it to the *vesuvianum*-type are seen in *St. confluens*. Johnson's section *Botryoideum* (syn. sect. *Verruculata* Satô) is of value if restricted to the species with coralloid phyllocladioid branchlets, and the sect. *Sacculata* of Satô undoubtedly designates a very natural grouping within the genus and is worthy of retention. Körber's section *Eustereocaulon* is a convenient repository for a large number of the boreal species with true phyllocladia, but his section *Cereolus* (syn. *Prostereocaulon* of Riddle) is too vague in its application to be of much practical value. On the other hand, Nylander's genus *Stereocladium*, emended so as to include only *St. tyroliense*, should be retained as a monotypic section for that species. The section *Chondrocaulon* of Th. Fries (syn. *Leprocaulon* of Nylander) may be used to accommodate *St. quisquiliare*, *St. arbuscula*, and *St. albicans*, also probably *St. congestum*, but it must be admitted that the latter species can hardly be separated morphologically from the *Eustereocaulon* group.

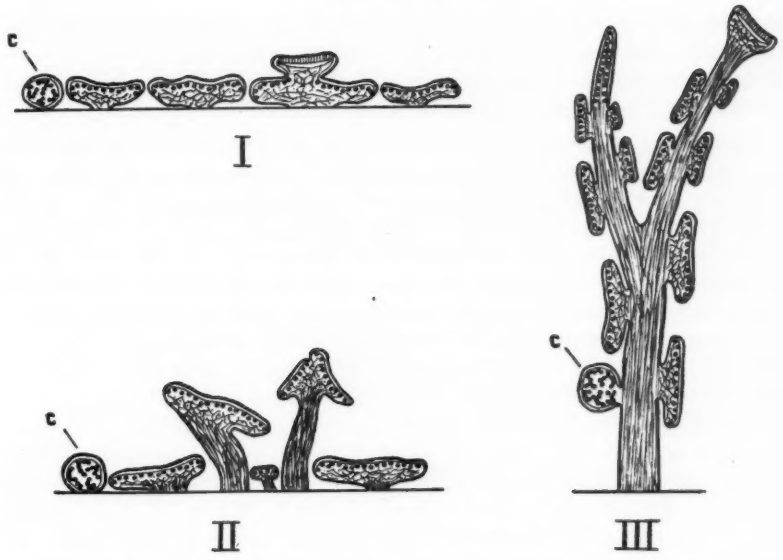
From the data presented in the foregoing pages it would appear that the major natural division in *Stereocaulon* is between those species on the one hand in which the pseudopodetia are formed by the extension of all layers of the primary thalline bullae or areolae, and in which the function of assimilation is carried out by terete branches of the pseudopodetium (phyllocladioid branchlets), and those on the other hand in which only the basal medullary tissue of the primary thalline squamules goes to form the pseudopodetia, the phyllocladia being true phyllocladia of variously squamulose form usually identical with those of the primary thallus. These two major types may be distinguished as subgenera, with the proposed names *Holostelidium* and *Enteropodium* respectively. The type species of subgen. *Holostelidium* is *St. sorediiferum* Hue, that of subgen. *Enteropodium St. paschale*. Text-figs. 6 and 7 are diagrammatic representations of the course of ontogenetic development in the two subgenera.

The subgenus *Holostelidium* is recognizable by the terete-coralloid phyllocladioid branchlets. Besides the type species *St. sorediiferum*, it contains the



TEXT-FIG. 6. Schematic representation of ontogenetic and phylogenetic development in *Stereocaulon* subgen. *Holostelidium*.

I. hypothetical ancestral form with a crustose thallus of corticate bullose areolae.
II. orthotropic elongation of all layers of the thallus giving rise to simple corticate pseudopodetia.
III. harmonic branching of the corticate pseudopodetia.
IV. disharmonic development of the branches to form phyllocladioid branchlets.
V. loss of the cortical and algal strata except on the phyllocladioid branchlets.
(*c*, cephalodium.)



TEXT-FIG. 7. Schematic representation of ontogenetic and phylogenetic development in *Stereocaulon* subgen. *Enteropodium*.

I. hypothetical ancestral form with a crustose thallus of corticate squamulose areolae.
II. elevation of the thalline squamules as phyllocladia on ecorticate pseudopodetia formed by the elongation of the lower medullary tissue.
III. elongation and branching of the pseudopodetia with formation of secondary lateral phyllocladia.
(*c*, cephalodium.)

well known *St. ramulosum*, and also *St. claviceps*, *St. exutum*, *St. nesaeum*, *St. strictum*, *St. virgatum*, etc. It may be subdivided into the following six sections: *Redingeria* M. Lamb (n. sect.), with persistently simple or subsimple pseudopodetia devoid of phyllocladioid branchlets, and cephalodia of more or less distinctly defined sacculate structure (type species *St. caespitosum*); *Pilophoropsis* M. Lamb (n. sect.), with subsimple to slightly branched pseudopodetia provided with a few rudimentary phyllocladioid branchlets, and cephalodia of botryose structure (type and only known species *St. curtum*);* *Botryoideum* Johns., with branched pseudopodetia bearing numerous well defined disharmonic phyllocladioid branchlets, and botryose cephalodia (type species *St. exutum*); *Sacculata* Satô, with branched pseudopodetia bearing phyllocladioid branchlets, and sacculate cephalodia (type species *St. sorediiferum*); *Dactyloideum* M. Lamb (n. sect.) with digitate-lobate cephalodia resembling phyllocladia, as shown in Text-fig. 3, p. 536 (type species *St.*

* *In spite of its botryose cephalodia,* St. curtum *cannot, on morphological and phytogeographical grounds, be included in the sect.* Botryoideum, *but must form a monotypic section of its own. Its obvious affinities are with* St. caespitosum *and* St. gregarium *of the sect.* Redingeria.

strictum, syn. *St. peladense*); and *Ecephalodiata* M. Lamb (n. sect.) in which cephalodia are absent (type species *St. virgatum*). This last section *Ecephalodiata* may contain some species in which cephalodia may eventually be found, in which case these species would be redistributed to other sections.

The species of the sect. *Sacculata* may be divided into two natural subsections on the basis of their spore structure. In one group the spores are relatively short, fusiform-cylindrical, and pauciseptate (septa 3-7); in the other they are longer, vermiform, and multiseptate, with (7-) 8-30 septa. These two divisions were distinguished in manuscript by Du Rietz (in an unpublished list of species seen by the author at Uppsala) as *Aciculisporae* and *Ascaridisporae* respectively, which names, with the original author's permission, may be used for the two subsections thus designated. The type species of subsect. *Aciculisporae* is *St. ramulosum*, that of subsect. *Ascaridisporae St. sorediiferum*.

The subgenus *Enteropodium* may be divided into four sections as follows: *Chondrocaulon* Th. Fr., with the pseudopodetia thin, cartilaginous, more or less leprarioid; apothecia and cephalodia unknown (type species, *St. quisquiliare*); *Eustereocaulon* Körb. (including *Prostereocaulon* of Riddle), with the pseudopodetia stouter, not cartilaginous nor leprarioid; cephalodia and apothecia commonly developed; phyllocladia without darker centers (type species, *St. paschale*; this section includes also the majority of the boreal species of the genus, including *St. coralloides*, which in spite of the coralloid appearance of its phyllocladia belongs here and not to the subgen. *Holostelidium*; see page 529); *Stereocladium* (Nyl.) Dodge (emend.), containing the single species *St. tyroliense*, which differs from all other species in having the squamules of its primary thallus of a type different from those which form the phyllocladia on the pseudopodetia; and *Leucocheilon* M. Lamb (n. sect.), distinguished by peltate or compressed-ramiform phyllocladia usually with paler margins and darker central part, the latter consisting of hyaline, gelatinized tissue (type species, *St. vesuvianum*).

This last section *Leucocheilon* falls naturally into two distinct subsections: *Peltophyllum* (DR.) M. Lamb (syn. ser. *Peltophyllae* DR. in mscr. ined.), with the phyllocladia peltate and lateral on the pseudopodetia (type species, *St. vesuvianum*), and *Phyllocaulon* (Tuckerm.) M. Lamb, with the phyllocladia in the form of flattened apical expansions of the pseudopodetia (type species, *St. Wrightii*).

The proposed classification may be tabulated as follows:

Genus *Stereocaulon* (Schreb.) Hoffm.

Subgen. I. *Holostelidium* M. Lamb (n. subgen.). Pseudopodetia e crescentia stratorum omnium areolarum thalli primarii orta; ramuli phyllocladioidei vulgo adsunt, phyllocladia vera nulla. Typus subgeneris: *St. sorediiferum* Hue.

Sect. 1. *Redingeria* M. Lamb (n. sect.). Pseudopodetia simplicia vel subsimplicia; ramuli phyllocladioidei desunt; cephalodia obsolete vel satis distincte sacculata. Typus sectionis: *St. caespitosum* Redgr. Huc etiam pertinet *St. gregarium* Redgr.

Sect. 2. *Pilophoropsis* M. Lamb (n. sect.). Pseudopodetia subsimplicia aut modice ramosa; ramuli phyllocladioidei parum evoluti; cephalodia botryosa. Typus sectionis et species unica cognita: *St. curtum* (Räs.) M. Lamb.

Sect. 3. *Botryoideum* Johns. emend. M. Lamb. Pseudopodetia vulgo bene ramosa; ramuli phyllocladioidei numerosi, perfecte evoluti; cephalodia eximie botryosa. Typus sectionis: *St. exutum* Nyl. Huc etiam pertinent: *St. curtatum* Nyl., *St. japonicum* Th. Fr., *St. octomerellum* Müll. Arg., *St. octomerum* Müll. Arg., *St. pendulum* Asah., *St. prostratum* Zahlbr., *St. verruculigerum* Hue.

Sect. 4. *Sacculata* Satô. Pseudopodetia vulgo bene ramosa; ramuli phyllocladioidei vulgo numerosi et perfecte evoluti; cephalodia sacculata. Typus sectionis: *St. sorediiferum* Hue.

Subsect. A. *Aciculisporae* DR. ex M. Lamb (n. subsect.). Sporae fusiformi-cylindricae, pauciseptatae, septis 3-7. Typus subsectionis: *St. ramulosum* (Sw.) Räusch. Huc etiam pertinent: *St. Argus* Hook. f. & Tayl. emend. Th. Fr., *St. corticatulum* Nyl., *St. implexum* Th. Fr., *St. Meyeri* Stein, *St. pachycephalum* Vain., *St. pilophoroides* Tuck., *St. roccelloides* Th. Fr.

Subsect. B. *Ascaridisporae* DR. ex M. Lamb (n. subsect.). Sporae vermiformes, multiseptatae, septis (7-) 8-30. Typus subsectionis: *St. sorediiferum* Hue. Huc etiam pertinent: *St. botryophorum* Müll. Arg., *St. claviceps* Th. Fr., *St. foliolosum* Nyl., *St. macrocephalum* Müll. Arg., *St. nesaeum* Nyl., *St. piluliferum* Th. Fr., *St. sinense* Hue.

Sect. 5. *Dactyloideum* M. Lamb (n. sect.). Cephalodia digitato-lobata, pallida, ad instar phyllocladiorum. Typus sectionis: *St. strictum* Th. Fr. (syn. *St. peladense* Vain.). Huc etiam pertinet *St. explanatum* M. Lamb (syn. *St. proximum* var. *compressum* Nyl.).

Sect. 6. *Ecephalodiata* M. Lamb (n. sect.). Cephalodia desunt. Typus sectionis: *St. virgatum* Ach. Huc etiam pertinet *St. scutelligerum* Th. Fr.

Subgen. II. *Enteropodium* M. Lamb (n. subgen.). Pseudopodetia e crescentia tantum strati medullaris basalis areolarum thalli primarii orta; phyllocladia vera evoluta, iis thalli primarii similia. Typus subgeneris: *St. paschale* (L.) Hoffm.

Sect. 1. *Chondrocaulon* Th. Fr. Thallus primarius haud observatus. Pseudopodetia tenera, cartilaginea, plus minusve leprosa; cephalodia apotheciaque ignota. Typus sectionis: *St. quisquiliare* (Leers) Hoffm. Huc etiam pertinent: *St. albicans* Th. Fr. emend. M. Lamb, *St. arbuscula* Nyl., *St. congestum* Nyl., *St. pseudoarbuscula* Asah., *St. tenellum* Tuck.

Sect. 2. *Eustereocaulon* Körb. Thallus primarius persistens aut evanescens, e squamulis verrucisve constans phyllocladiis pseudopodetiorum similibus; pseudopodetia valida, haud cartilaginea, vulgo haud leprosa; cephalodia apotheciaque vulgo evoluta; phyllocladia sine centro obscuro. Typus sectionis: *St. paschale* (L.) Hoffm. Huc pertinent complures species boreales, viz.: *St. botryosum* Ach. emend. Frey, *St. capitellatum* H. Magn., *St. condensatum* Hoffm., *St. coralloides* Fr., *St. Delisei* Bory, *St. Depreaultii* Del. ex Nyl., *St. evolutoides* (H. Magn.) Frey, *St. evolutum* Graewe, *St. glareosum* (Sav.) H. Magn., *St. hypopetraeum* Vain. ex Räs., *St. incrustatum* Flk., *St. intermedium* (Sav.) H. Magn., *St. nanodes* Tuck., *St. Ostrobottniae* H. Magn., *St. pileatum* Ach., *St. rivulorum* H. Magn., *St. subcoralloides* Nyl., *St. tennesscense* H. Magn., *St. tomentosum* Fr.; necnon species nonnullae exoticae, e. gr. *St. sphaerophoroides* Tuck., *St. supervestiens* H. Magn.

Sect. 3. *Stereocladium* (Nyl.) Dodge emend. M. Lamb. Thallus primarius persistens, e squamulis constans erectis, flabellato-spathulatis; pseudopodetia (rarius perfecte evoluta) sat valida, haud cartilaginea; phyllocladia vera pseudopodetiorum granulosa, sine centro obscuro. Cephalodia vulgo evoluta, apothecia interdum prolata. Typus sectionis et species unica cognita: *St. tyroliense* (Nyl.) Zahlbr.

Sect. 4. *Leucocheilon* M. Lamb (n. sect.). Thallus primarius persistens aut evanescens, e squamulis constans phyllocladiis pseudopodetiorum similibus; pseudopodetia valida, haud cartilaginea, vulgo haud leprosa; cephalodia apotheciaque vulgo evoluta; phyllocladia peltata aut compresso-ramosa, vulgo margine pallidiore et parte centrali obscuriore (e hyphis hyalinis gelatinosis formata). Typus sectionis: *St. vesuvianum* Pers.

Subsect. A. *Peltophyllum* (DR.) M. Lamb (n. subsect.). Phyllocladia lateralia, sessilia, peltata. Typus subsectionis: *St. vesuvianum* Pers. Huc etiam pertinent: *St. confluens* Müll. Arg., *St. cornutum* Müll. Arg., *St. farinaceum* H. Magn. (ut videtur), *St. flavireagens* Gyeln., *St. gracillimum* Müll Arg., *St. graminosum* Schaer., *St. lavicola* H. Magn. emend. M. Lamb, *St. leprocephalum* Vain., *St. pityrizans* Nyl., *St. Saviczii* DR., *St. violascens* Müll. Arg., *St. Vulcani* (Bory) Ach.

Subsect. B. *Phyllocaulon* (Tuck.) M. Lamb. Phyllocladia apicalia, complanata, ramoso-expansa. Typus subsectionis: *St. Wrightii* Tuck. Huc etiam pertinere videntur: *St. Maunae-Loae* H. Magn., *St. platycladum* (M. Lamb) M. Lamb.

Phytogeographical Considerations

In all hypotheses relating to the phylogeny of a genus, and in all attempts to construct a system of natural subgenera and sections, it is necessary to call into account the spatial correlations shown by the various taxonomic entities in their past and present areas of distribution, because such phytogeographical evidence provides an excellent check on taxonomic subdivisions made on morphological grounds. As most of the basic types of plant distribution in the world are now known with a fair degree of accuracy,* it should be possible in the majority of cases to place a natural taxonomic unit into a known distributional category concordant with the known facts of origin and migration. As is now well known, lichens show the same types of areas and disjunctions as do the flowering plants, in spite of their apparently greater intrinsic capacity for long-distance dissemination by minute air-borne diaspores.

Taking the present genus, it is at once obvious that many of the arbitrary and unnatural subgeneric categories criticized on pp. 559-561 of the present paper would, on plotting cartographically, reveal their worthlessness by failing to show distributional areas of a logically explainable type. Truly natural subdivisions, on the other hand, should show definite areas from which certain conclusions as to their origin and subsequent migrations may be deduced, thus throwing additional light on the problems of phylogeny in the genus.

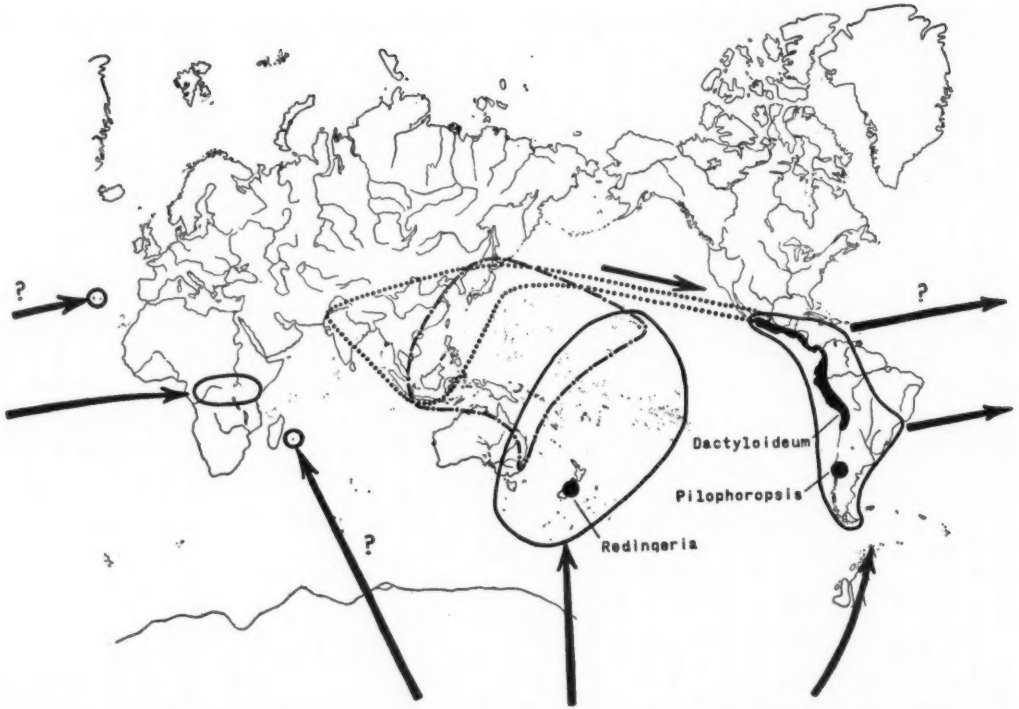
Anomalous and unexplainable types of distribution should not occur in higher taxonomic categories, such as families, genera, and subgenera; but in

* *See for instance v. Ihering, Die Phytogeographischen Grundgesetze, in Engler's Botan. Jahrb. 62 : 113 (1929); Hultén, Outline of the History of Arctic and Boreal Biota during the Quaternary Period (1937), and Atlas över Växternas Utbredning i Norden (1950); and Vester, Die Areale und Arealtypen der Angiospermen-Familien, in Botan. Archiv, 41 : 203, 295, 520 (1940).*

lower units, such as sections, species, and varieties, they are occasionally met with, for a variety of reasons. Firstly, we must consider the possibility of fortuitously convergent evolution in two widely separated areas; as regards species, whose delimitation rests on the sum total of a number of concordant characters, this must be regarded as highly improbable, but it may occur in categories defined on the basis of one or only a few characters. An example in the present genus which may be explained in this way is the species-pair *virgatum* and *scutelligerum*, widely and anomalously separated geographically (Antillean and Madagascarian regions), but agreeing closely in two characters, namely the small lateral apothecia and the absence of cephalodia. Secondly, the anomalous disjunction may rest on a mere weakness in the taxonomy, in that an accidental modification or ecotype, arising spontaneously in widely separated areas, may be endowed with the rank of a species. One may suspect that *St. confluens*, known from Africa, Java, and Norway (!), belongs to this category, although it is a clearly recognizable and apparently distinct morphological type of the *vesuvianum*-series. Lastly, one must be prepared occasionally to meet with hitherto unknown or imperfectly understood but genuine disjunctions, such as that afforded by *St. flavireagens*, which is certainly a good species and occurs in Hawaii, the Azores, and the Canary Islands; perhaps relict stations of an extensive Cretaceous range similar to that of the genus *Cocculus* (Menispermaceae), mentioned on p. 135 of v. Ihering's 1929 paper.

On account of limitations of space, no detailed distributional data for individual species can be given here; this must be reserved for later monographic treatment.

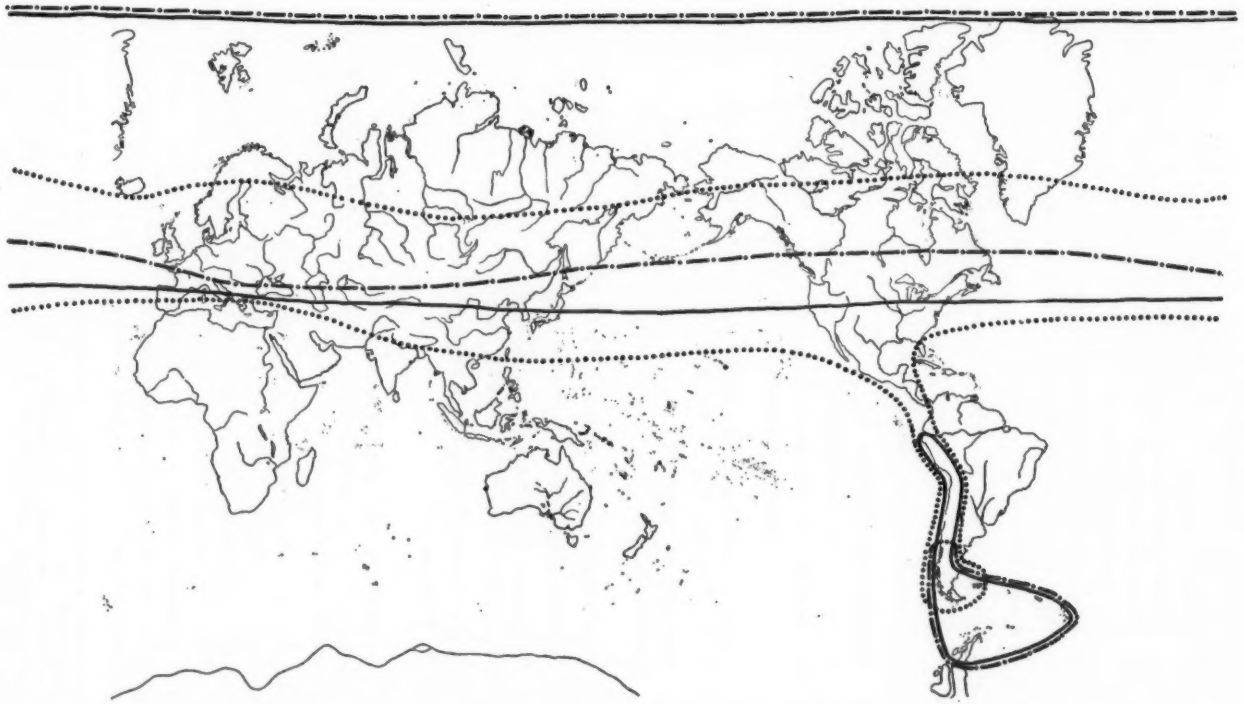
The subgenus *Holostelidium* (Text-fig. 8) is obviously of Southern hemisphere origin, and its most primitive living representatives (sects. *Redingeria* and *Pilophoropsis*) are today found as relicts in New Zealand and Patagonia. Therefore it seems probable that the subgenus originated as a palaeoaustral element in the Antarctic land-mass (Archinotis) in Cretaceous and Tertiary times, spreading from there northwards to S. America via Graham Land, and to the Australian region via the now submerged connection of which the present subantarctic islands of New Zealand are the sole remnants. From the Australian region a well defined section (*Botryoideum*) was evolved in E. Asia, with its center of speciation in Japan, migration having apparently been by way of Australia and the Malaysian archipelago, as indicated by relict areas in E. Australia, Java, and Formosa. This section *Botryoideum* also has an oceanic Pacific outlier in the Hawaiian islands (*St. octomerellum*). Another series of high morphological evolution (*Ascaridisporae*) was evolved in the E. Asiatic-Malaysian region, having apparently travelled thence from New Zealand via Malaysia to the Himalayan region, where the most active production of highly developed sporological types took place. A bifurcation of the migratory route seems to have occurred in Malaysia, one series of species penetrating northwards along what is now the Pacific coastline (Philippines and Formosa) to Japan. Possibly also a subsequent overland linkage was



TEXT-FIG. 8. Distributional areas of the sections and subsections of *Stereocaulon* subgen. *Holostelidium*. The arrows indicate the presumed routes of migration. Sect. *Sacculata:* Subsect. *Aciculisporae* = ————; Subsect. *Ascaridisporae* = ... ; Sect. *Botryoideum* = — · — · — ·

accomplished from the Himalayan region to Japan via the mountains of southern China in the case of *St. claviceps*, which belongs morphologically to the Himalayan complex, although to date it has not yet been found in the latter region. Finally, in one species (*St. claviceps*), a transoceanic connection was established in Tertiary times, via the hypothetical land-mass of Archigalensis, to America (Mexico). The series *Aciculisporae* has three species common to both the New Zealand and the S. American areas (*St. ramulosum*, *St. corticatulum*, and *St. implexum*, the latter represented in New Zealand by a vicarious variety), and hence probably originated on the ancient Antarctic continent of Archinotis. In the tropical Cordillera of S. America it seems to have given rise to the Andine section *Dactyloideum* and perhaps to the Venezuelan-Antillean species *St. virgatum*. It is represented in Hawaii (partly by endemic species or varieties), having presumably migrated thence from the Australian region by way of the islands of Oceania. Furthermore it is present in the African region, in the mountains of tropical Africa, and the Madagascarian islands, migration most probably having been in the first instance from S. America ("Archhelenis"-connection); in the second either from the Australian region via the ancient Indo-Australian continent of Lemuria, or possibly directly from Antarctica by way of Kerguelia. *Stereocaulon* does not, to the author's knowledge, exist in Kerguelia at the present day, but the related genus *Argopsis*, which is obviously derived from *Stereocaulon* subgen. *Holostelidium*, is of similar Antarctic origin, and occurs both in Kerguelia and the subantarctic islands of New Zealand, so that there was quite possibly a trifurcate radiation of the *Aciculisporae* northwards, to colonize the Australian region, S. America, and, by using the Kerguelean route, the Madagascarean region. One species of this section occurs in the Azores (*St. Meyeri*), this being the northernmost known extension of the section in the Northern hemisphere; the species in question is found both in South and Central America and in E. Africa. Distribution of the latter type, if we exclude the possibility of long-distance dispersal, seems adequately explainable only on the basis of the Eocene Archatlantis-connection postulated by v. Ihering.

The subgenus *Enteropodium*, in contrast to *Holostelidium*, which we have seen to be of austral, probably of Antarctic origin, has, apart from the sections *Chondrocaulon* and *Leucocheilon*, which are considered separately below, certainly arisen from a boreal stock, although three of its representatives (*St. botryosum*, *St. paschale*, and *St. tomentosum*) have migrated to the Southern hemisphere, probably as part of the "Stephanoflora" of Cretaceous and Tertiary times, and are today found also in the S. American sector (Text-fig. 9). The morphologically most primitive representatives of subgen. *Enteropodium* (*St. condensatum*, *St. glareosum*, and *St. pileatum*) are boreal species not found in the Southern hemisphere. Generally speaking, the subgenus is boreal–arctic–circumpolar in its distribution, showing the variations on this basic type already well known in other groups of plants. We can, for instance, distinguish the following phytogeographical elements within the subgenus:



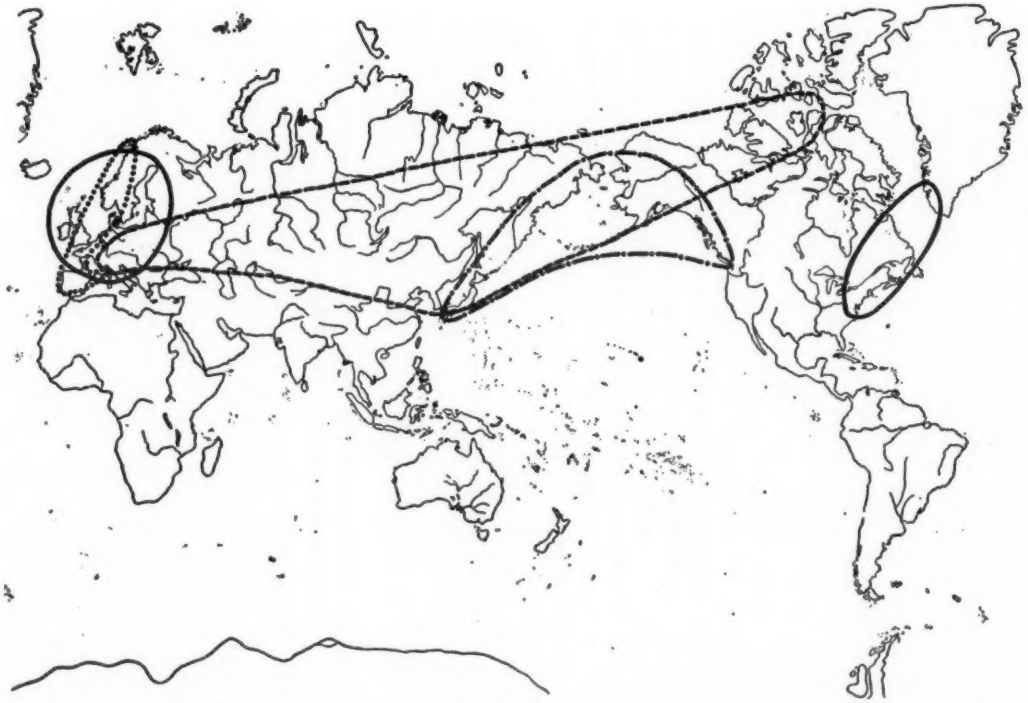
TEXT-FIG. 9. Distributional areas of *Stereocaulon paschale*, *St. botryosum*, and *St. tomentosum*, three species of the subgen. *Enteropodium* which have penetrated into the Southern hemisphere in the S. American sector. —— = *St. paschale*; — · — · — = *St. botryosum*; · · · · · · = *St. tomentosum*.

1. *The Continuously Circumpolar Element*
   - A. With bipolar extension to the S. hemisphere in S. America.
     - a. Arctic–montane in the N. hemisphere; extending into the Antarctic continent in the S. hemisphere: *St. botryosum*; *St. paschale* (Text-fig. 9).
     - b. Boreal–montane in the N. hemisphere; not extending into the Antarctic continent in the S. hemisphere: *St. tomentosum* (Text-fig. 9).
   - B. Restricted to the N. hemisphere: *St. glareosum*; probably *St. rivulorum.*
2. *The Incompletely Circumpolar Element*
   - A. Amphiatlantic species.
     - a. Arctic: *St. capitellatum.*
     - b. Boreal: *St. coralloides* (Text-fig. 10); *St. evolutoides*; *St. pileatum*; probably *St. condensatum.*
   - B. Eurasiatic species, partly extending into N. America: *St. incrustatum* (Text-fig. 10); *St. subcoralloides.*
   - C. Beringian bilateral radiants: *St. intermedium* (Text-fig. 10); *St. Saviczii*: Ch. str. II ("Sasakii"-strain) of *St. tomentosum.*
3. *The European-Atlantic Element*: *St. Delisei*; *St. evolutum* (Text-fig. 10).
4. *The European Arctic-montane Element: St. (Stereocladium) tyroliense.*
5. *The Macaronesian Element* (Canary Islands, Madeira, Azores, an early Tertiary outlier of the Palaeo-boreal flora): *St. sphaerophoroides.*
6. *Endemics of doubtful origin: St. supervestiens* (Hawaii); *St. tennesseense* (U.S.A., Tennessee).*

Further distributional and phylogenetic data will be necessary to throw light on the question of the probable focus of origin of the subgenus *Enteropodium* in the Northern hemisphere.

As regards the sect. *Chondrocaulon*, the richest development of species is in the S. American Cordilleran–Pacific region, but representatives are found in a number of other regions also in a remarkably disjunct distributional pattern (Cuba, S. Africa, Mauritius, Himalaya, Japan, Samoa, W. Canada, Greenland), which indicates either polyphyletic constitution (a not improbable hypothesis, since the section is an assemblage of "imperfect" species defined on thalline characters only) or else great evolutionary antiquity coupled with

* St. tennesseense, *according to the author's examination of the type material, is closely related to the Beringian radiant species* St. intermedium. *Therefore it is perhaps to be regarded as a relict species belonging to the group with disjunct Asiatic – E. North American distribution, of which* Umbilicaria caroliniana *Tuck. is a good example (see the remarks of Llano in J. Wash. Acad. Sci. 41: 199. 1951).*



TEXT-FIG. 10. Distributional areas of four boreal species of *Stereocaulon* subgen. *Enteropodium: St. coralloides* (amphiatlantic element), *St. evolutum* (European–Atlantic element), *St. intermedium* (Beringian bilateral radiant), and *St. incrustatum* (Eurasiatic element with extension to the Canadian Arctic archipelago). ——— = *St. coralloides;* . . . . . = *St. evolutum;* — · — · — = *St. intermedium;* — — — —*St. incrustatum.*

wide environmental tolerance. *St. quisquiliare* shows an interesting bicontinental distribution, being known from Europe and *Western* N. America (California and Washington).

The section *Leucocheilon* shows no distinct world areas of particularly active speciation, and its members are effusely distributed over practically all parts of the globe. There is however a distinct correlation with the volcanic regions of the world in the majority of the species, which are characteristic lava flow pioneers. Some of the species and varieties are not edaphically bound to lava flows, but grow on plutonic and metamorphic rocks and even on soil, but numerically they are in the minority and do not comprise the most primitive species of the section; this seems to indicate the origin of sect. *Leucocheilon* in regions of high vulcanicity, with secondary ecological modification of some of the species and varieties to substrata other than lava, this permitting their subsequent spread to nonvolcanic regions. Among the lavicole species of the section, no particular regional center can be discerned in either hemisphere. Accordingly it seems that we must postulate the origin of sect. *Leucocheilon* from a very ancient and widespread syngameon of volcanic regions. A number of endemic island species have been produced in this section (*St. cornutum*, *St. gracillimum*, *St. graminosum*, *St. lavicola*, *St. Vulcani*), and some remarkable insular disjunctions, like that of *St. flavireagens* mentioned above (Hawaii—Azores and Canary Islands). *St.* (*Phyllocaulon*) *Wrightii* is an excellent example of a Beringian radiant, occurring in the Bering Straits islands, N. E. Siberia, and Japan, and *St. leprocephalum* may represent a wider extension of the same type (N. E. Siberia and E. Arctic Canada, probably to be found also in other parts of the Canadian Arctic archipelago). Present day persistence on nunataks of inland ice is exemplified in one of the species of this section (*St. platycladum*).

The Evolution of Stereocaulon from Primitive Forms and Its Natural Position in the Lichen System

Stereocaulon, among other lichen genera, is characterized by the fruticulose elongation of its thalline tissue into an extended, usually dendroid form. As Reinke has pointed out (39), this is in the lichens a response to the need for greater development of surface area for purposes of photosynthesis, and from this we may conclude that the symbiotic mode of life in consortium with green algae was already well established in the hypothetical crustaceous ancestral states, this adaptation to assimilation of carbon dioxide supplying the impetus to the later fruticulose development. The nonlichenized Discomycetes which have evolved erect habitus, e.g. *Morchella*, *Helvella*, *Mitrula*, etc., have done so in response to a quite different causal factor, namely the need for more efficient spore-production and dissemination.

Undoubtedly therefore the ancestral states of *Stereocaulon* were already true lichens, similar to the crustaceous lichens in existence at the present day. The persistence of the crustaceous habit in many families of lichens indicates that continued modification of thalline structures for greater photosynthetic

efficiency is not an automatic process but must depend on the genetic plasticity of the particular group in question, i.e. on the possibility of mutations and gene-recombinations which furnish the variations upon which the selective factors may operate to bring about the production of new morphological types. These selective factors may be either internal (concerned with metabolism and propagation) or external (environmental). Groups and genera of unstable genetic constitution may be expected to evolve more rapidly into more efficient somatic forms; when these modifications have been accomplished, and an approximation made to the ideal form in the functional sense, continued genetic instability will produce numbers of purely fortuitous variations, many of them worthy of the rank of separate species or even genera, but which have no adaptive significance; "a mere frill of variety superimposed upon its broad pattern", to quote the words of Huxley (18, p. 389). Most groups appear to attain some degree of genetic stability at a certain stage in their evolution, and ancestral forms which have in the past given rise in parts of their distributional areas to more highly developed groups may persist more or less unchanged and exist contemporaneously with the latter. The reason for this may perhaps be sought in hybridization in a limited area or in collision of the ancestral form with genetically disrupting environmental influences at the boundaries of its natural habitat.

It is therefore not improbable that certain lichens still existing at the present day, and arrested at different stages in their phylogenetic development, may furnish a series of links connecting *Stereocaulon* with its hypothetical crustaceous ancestors. This is the view held by Nilson (Kajanus) (21, 23), who derives *Stereocaulon* from *Toninia*, *Thalloidima*, and ultimately *Catillaria*, and places all these genera together, with *Argopsis*, in a natural grouping called *Catillariales*.

Nilson agrees with Vainio that the podetial structures in *Stereocaulon* are pseudopodetia, i.e. are derived from thalline and not apothecial tissues, and that *Stereocaulon* is for this reason not closely related to the genera of the Cladoniaceae (*Cladonia*, *Baeomyces*, *Pilophoron*, etc.). He considers that the genus *Toninia* represents the most likely ancestral condition for *Stereocaulon*, as in certain species it manifests a distinct tendency towards fruticulose development. This fact was already pointed out by Reinke (39), although the latter did not deduce any phylogenetic relationship between the two genera; Reinke's illustration of *Toninia* (*Thalloidima*) *coeruleonigricans* (syn. *Thalloidima vesiculare*) in Fig. 32, vii of the work quoted, showing an old thallus with development of stipelike lobes, shows a striking resemblance to the primitive phyllocladioid pseudopodetia of *Stereocaulon caespitosum*; in fact, Reinke says of it: "die sterilen Aeste sind die Anfänge von Phyllocladien".

Continued fruticulose development of a thallus similar to that of *Toninia coeruleonigricans*, i.e., consisting of rounded, bullate, verrucose areolae, would give rise to a form similar to *Stereocaulon caespitosum* and thence to the highly branched state characteristic of other *Stereocaulon* species. The elongation

would comprise all the tissues of the primary thalline bulla: cortex, medulla, and algal stratum, and would give rise to pseudopodetia of the *Holostelidium* type with phyllocladioid branchlets but no true phyllocladia.

For the *Stereocaula* of subgen. *Enteropodium* it is necessary to postulate an ancestral crustaceous condition of somewhat different character. It is an observed fact that in this subgenus the primary thallus, when present, consists almost always of squamules similar in form to the phyllocladia on the pseudopodetia. These squamules are usually more or less flattened, and not uncommonly lobed and crenated at their periphery. For an approximation to the hypothetical ancestral state of subgen. *Enteropodium*, therefore, it is necessary to search among the living representatives of *Toninia* possessing a thallus consisting, not of simple, smooth, subglobose bullae as in *T. coeruleonigricans*, but of more or less flattened and crenated squamules. An obvious example of such a species is afforded by *Toninia* (*Eutoninia*) *syncomista* (Flk.) Th. Fr.; if this species were to develop fruticulose habitus, the formation of the stipes would have to be limited to the basal medullary layer of the squamules, because their foliose form and crenation would preclude the possibility of simultaneous elongation of all the tissues composing them. In other words, the fruticulose development would be of the *Enteropodium* type, not of the *Holostelidium* type, and the squamules, raised up on the naked medullary stipes (pseudopodetia) would conserve their original form and would in fact represent true phyllocladia. An example of this type of development actually occurring in living representatives of the genus *Toninia* is apparently seen in *T.* (*Eutoninia*) *squalida* (Schleich.) Mass. and *T. verruculosa* (Th. Fr.) Vain., in which the assimilative squamules are located at the apices of naked (non-assimilative) stipes of medullary origin which penetrate downwards into the substratum.

A very suggestive resemblance between a living *Toninia*-species and *Stereocaulon* is found in *T.* (*Eutoninia*) *leucophaeopsis* (Nyl.) Th. Fr. This species is characterized by bicolorous squamules of peltate or crenate-squamulose form, with more or less tumid whitish margins and a darker, somewhat depressed central area; the resemblance to phyllocladia of the *Stereocaulon vesuvianum*-group (subgen. *Enteropodium*, sect. *Leucocheilon*) is striking even on superficial examination. Through the courtesy of Dr. W. Watson (Taunton) a specimen of this species collected by him in Wales (under the name of *Toninia cambrica* (Wheld.), which appears to be synonymous with *T. leucophaeopsis*) was received and examined microscopically for the details of its thalline structure, concerning which no data were previously available. The anatomical features also were found to be in close agreement with those of the peltate phyllocladia of *Stereocaulon vesuvianum* (*denudatum*); the darker central part being composed of colorless, hyaline, and transparent tissue in the form of a bowl-shaped inclusion consisting of highly gelatinized and completely confluent hyphae, with only the fistulose lumina visible in the common gelatinous matrix. The light colored margins, as in *Stereocaulon*

vesuvianum, were composed of a sordid yellowish-nubilated cortex of indistinctly paraplectenchymatic structure. The resemblance therefore, both morphological and anatomical, between the squamules of *Toninia leucophaeopsis* and the phyllocladia of the *vesuvianum*-group of *Stereocaulon* is so close that their common derivation is indicated with a high degree of probability. In fact, the subsp. *santorinense* of *St. vesuvianum*, in which pseudopodetia are hardly developed, and the apothecia are formed directly on the squamules of the primary thallus, is outwardly astonishingly similar to *Toninia leucophaeopsis*. The specimen of the latter investigated however did not give the orange-red paraphenylenediamine reaction (stictic acid) which is commonly found in the *Stereocaula* of the *vesuvianum*-group; but it should be mentioned that there is a Ch. str. II of *St. vesuvianum* containing lobaric acid which also gives no orange reaction with paraphenylenediamine.

The almost constant occurrence of cephalodia in *Stereocaulon* (except in the sections *Chondrocaulon* and *Ecephalodiata*), and their absence, so far as is known, in living species of *Toninia*, shows that probably no particular *Toninia*-species now in existence can be regarded as the immediate ancestor of *Stereocaulon*. The almost universal occurrence of cephalodia in the latter genus indicates that they must have been developed at an early stage in its evolution, most probably in the ancestral toninioid condition before fruticulose development had begun to take place. In *Stereocaulon* itself we can trace the gradual migration of the cephalodia from the primary thallus onto the pseudopodetia, as in the series *condensatum–pileatum–glareosum*, and *caespitosum–ramulosum*. Their absence in *Chondrocaulon* may be explained by the probably polyphyletic origin of this section (see below); in the sect. *Ecephalodiata* they seem to have been lost by secondary reduction. It therefore appears necessary to postulate a hypothetical ancestral condition, no longer in existence, resembling the modern *Toniniae* of the *coeruleonigricans*- and *syncomista*-groups, but provided with cephalodia between the thalline bullae or squamules. The nearest approach to such a condition is perhaps found in *Toninia leucophaeopsis* mentioned above, in which the thalline squamules are apparently constantly embedded in a black stratum consisting of Cyanophyceous algae (mainly *Stigonema* and *Gloeocapsa*), which may represent the forerunners of true cephalodia.

Some degree of polyphyletic diversity is apparent far back in the ancestry of *Stereocaulon*. The sect. *Chondrocaulon* is obviously of distinct origin, and its inclusion in the genus *Stereocaulon* is indeed only a provisional one, as its sporological type is as yet unknown. Apothecia and spores have been recorded for *St. quisquiliare* by Anders (1, p. 120), but confirmation is desirable, since they may possibly have belonged to a parasite, or the species may have been wrongly determined. Groenhart (17) suggests that these leprarioid "imperfect" species should be placed, as a separate genus *Leprocaulon*, in the family Chrysothricaceae. Among the undoubtedly genuine *Stereocaula*, the divergence between the subgenera *Holostelidium* and *Enteropodium* must have been apparent already in the ancestral crustaceous condition, on account of

the basic difference in form between the two thallus types: rounded simple bullae in the prototypes of *Holostelidium*, and flattened crenulate squamules in those of *Enteropodium*. The species of sect. *Leucocheilon* are also obviously derived from a third distinct prototype of crustaceous habit with peltate, bicolorous, darker-centered squamules, similar to those of the present-day *Toninia leucophaeopsis*. To this extent therefore the genus *Stereocaulon* may be said to be polyphyletic in its origin, in that some of its main subgeneric or sectional divisions originated from related but morphologically distinct species of the same ancestral toninioid genus, and this, as has been shown in the previous section, is in accordance with the phytogeographical data concerning the spatial origins and migration of these groups.

Finally, the question arises as to the most natural disposition of the genus *Stereocaulon* in the existing lichen system. Nilson's grouping of Catillariales, which includes the series *Catillaria–Toninia–Stereocaulon–Argopsis* (the latter dictyosporous genus being obviously directly derived from *Stereocaulon*), while it expresses with a high degree of probability a natural phylogenetic relationship, is too comprehensive in its scope to be used as a family in the modern sense, although possibly it should be retained for a higher taxonomic category, e.g. a natural order. The boundary between the living representatives of *Stereocaulon* and *Argopsis* on the one hand and *Catillaria* and *Toninia* on the other has now become so distinct that they can hardly be included together in one family. If *Catillaria* and *Toninia* are accordingly separated, they seem to be best accommodated in the family *Lecideaceae* according to the Zahlbrucknerian system (Engler & Prantl, Nat. Pflanzenfam.), for *Catillaria* merges by imperceptible gradations in its sporological characters into *Lecidea*. *Stereocaulon* and *Argopsis* should be regarded as the representatives of a distinct family, *Stereocaulaceae*, as has already been suggested by Räsänen (37) and some previous authors, for example Savicz (42). In any case, in the light of the morphological and phylogenetic evidence now available, these two genera can no longer be included in the family *Cladoniaceae* where they are placed in the system of Zahlbruckner.

Summary

The podetial structures in *Stereocaulon* are pseudopodetia, i.e., are of thalline, not of carpogenic origin. They may originate (*a*) by the elongation of all tissues (cortex, algal stratum, and medulla) of verrucae or bullae of the primary thallus, or (*b*) by the elongation of only the basal medullary layer of squamules of the primary thallus. On the basis of this difference, *Stereocaulon* is divided into two new subgenera, (*a*) *Holostelidium* and (*b*) *Enteropodium*.

In subgen. *Holostelidium* the function of assimilation is carried out by branchlets of the pseudopodetium (phyllocladioid branchlets). In the more primitive species the pseudopodetium has a continuous layer of cortex and symbiotic algae, and the phyllocladioid branchlets are harmonic, indistinguishable from ordinary pseudopodetial branches; in the more highly developed

forms the phyllocladioid branchlets become more numerous, smaller, and disharmonic, this being a response to the need for increased surface area for carbon dioxide assimilation on the part of the symbiotic algae. At the same time, the cortex and algal stratum tend to disappear from the main axis of the pseudopodetium, remaining only on the phyllocladioid branchlets, which are now specialized assimilative organs.

In subgen. *Enteropodium* the function of assimilation is carried out by true phyllocladia, which are squamules of the primary thallus carried up on the summits and sides of naked pseudopodetial stipes of medullary origin. They are usually similar in form to those composing the primary thallus.

Cephalodia appear to have been acquired at an early stage in the phylogenetic history of the genus, in all probability already in the ancestral crustaceous condition.

The three basic types of cephalodium distinguished by Johnson (19), "spherical", "botryose", and "scrobiculate", are discussed. The difference between the first two is found to be one of degree only, and they are connected by imperceptible gradations. The term "sacculate" is preferred to "scrobiculate", since not all cephalodia of this type are scrobiculate-foveolate.

Cephalodia of the sacculate type differ from those of the "spherical" and "botryose" types anatomically in the structure of their cortex. They may be either solid-cored or loose-cored. In some species a transition from cortex of the "botryose" type to that of the sacculate type has been observed. A comparative study of the anatomy of the pseudopodetial and cephalodial cortices in one of the most primitive living representatives of subgen. *Holostelidium* (*St. caespitosum*) indicates that cephalodia are most probably modified pseudopodetial or phyllocladioid structures. This view is supported by the discovery of a hitherto unobserved type of cephalodium of digitate form, closely resembling phyllocladia.

In the primitive *St. caespitosum* the pseudopodetium was found to possess two distinct types of cortex, one corresponding to that found in "botryose" cephalodia, the other to that found in sacculate cephalodia; it is suggested that in the prototypes of existing species one or other of these two types of pseudopodetial cortex was developed on the cephalodia, determining their further development as either botryose or sacculate.

The statistical correlations shown by Johnson (19) to exist between the type of cephalodium and increasing complexity of spore-form in *Stereocaulon* are analyzed and in general confirmed.

Simple, primitive cephalodia without distinct botryose division (the "spherical" type of Johnson) are found in the subgen. *Enteropodium*, where they may be observed in some species to become gradually botryose. Cephalodia of botryose form occur in some species of subgen. *Enteropodium*, but chiefly in a group of E. Asiatic species of subgen. *Holostelidium*, in which they attain their maximal development. Cephalodia of the sacculate type are found only in the subgen. *Holostelidium*.

The nature of the symbiotic Cyanophyceous alga in the cephalodium is not in itself a taxonomic character.

The apothecia of *Stereocaulon* are, so far as known, of protolecideine or superlecideine type, without participation of symbiotic algae.

Several structural types of apothecium described in boreal species, and formerly considered distinct, are reduced to developmental stages of the same fundamental type, arrested at various stages in different species.

Soredia are found constantly in certain species; in others they are inconstant and probably accidental. They may be farinose, formed by dissolution of the cortex and algal stratum, or granulose, formed by a gradual diminution in size of verruculose phyllocladia. Farinose soredia in constantly sorediate species occur on the ends of the pseudopodetia or phyllocladioid branchlets, or sometimes on the squamules of the primary thallus; in some species they are borne on one side of flattened bifacial expansions.

It is proposed to regard morphologically indistinguishable but chemically different lichen individuals as belonging to distinct chemical strains of the same species, and not as separate "chemical species", as has been a common practice hitherto. A list of the chemical compounds known to occur in *Stereocaulon* is given.

Previous subgeneric divisions of *Stereocaulon* are reviewed and most of them shown to be arbitrary and unnatural. A new classification is proposed on a phylogenetic basis, with the two subgenera *Holostelidium* and *Enteropodium* further divided into sections and subsections on characters derived from the cephalodia, the form of the pseudopodetia and phyllocladia, and the spores.

A phytogeographical analysis of the present day distribution of these proposed divisions confirms their general validity, as their areas are found to be in accordance with the generally accepted principles of plant migration and differentiation. The focus of origin of the subgen. *Holostelidium* is in the Southern hemisphere (probably the Antarctic continent); that of the subgen. *Enteropodium* (with the possible exceptions of sects. *Chondrocaulon* and *Leucocheilon*) is boreal.

An attempt is made to reconstruct the hypothetical crustaceous ancestral prototypes from which *Stereocaulon* has arisen. These ancestral conditions approximate closely to certain living species of the genus *Toninia*, which in turn has evolved from effusely crustaceous Catillarioid forms.

The natural position of *Stereocaulon* in the lichen system is accordingly next to the Lecideaceae, and not in the Cladoniaceae, where it has commonly been placed. *Stereocaulon* and the related dictyosporous genus *Argopsis* are best accommodated in a separate family, Stereocaulaceae, adjacent to the family Lecideaceae.

A list is given of the new taxonomic combinations and emendations made in the present paper.

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Appendix: New Combinations and Emendations

In the foregoing pages it has been necessary to refer to a number of species, some of which have had to undergo changes in rank or nomenclature as the result of type and taxonomic studies. For the benefit of systematists, all such changes introduced in the present paper are here collected together and enumerated in alphabetical order.

St. albicans Th. Fr., De Stereoc. et Pilophor. Comment. (1857) p. 36, *emend.* M. Lamb. Th. Fries cites two specimens in his original description, without specifying the type. These two specimens belong to distinct species, and *St. albicans* is therefore emended to include only one of them (that collected by Haenke). The other specimen, collected by Gaudichaud, is referable to *St. tenellum* Tuckerm.

St. botryosum Ach. *emend.* Frey var. *spathuliferum* (Vain.) M. Lamb, *n. comb.* (Syn. *St. spathuliferum* Vain. in Ark. f. Bot. VIII, no. 4 (1909) p. 36; *St. fastigiatum* f. *spathuliferum* H. Magn., Stud. Bor. Stereoc. (1926) p. 37). Although undoubtedly conspecific with *St. botryosum* (*fastigiatum*), it appears to deserve a higher status than that of a form.

St. corticatulum Nyl. var. *subcorticatum* (Räs.) M. Lamb, *n. comb.* (Syn. *St. subcorticatum* Räs. in Ann. Bot. Vanamo, II, no. 1 (1932) p. 24).

St. curtum (Räs.) M. Lamb, *n. comb.* (Syn. *St. macrocarpon* var. *curta* Räs. in Revista Universitaria, Santiago, XXII (1937) p. 200).

St. evolutoides (H. Magn.) Frey var. *saxatile* (H. Magn.) M. Lamb, *n. comb.* (Syn. *St. saxatile* H. Magn., Stud. Bor. Stereoc. (1926) p. 41).

St. explanatum M. Lamb, *nom. nov.* (Syn. *St. proximum* var. *compressum* Nyl., Synops. Lich. I (1860) p. 237; non *St. ramulosum* var. *compressum* Bab. apud Hooker, Bot. Antarct. Voy. Erebus and Terror, II, Flora Nov. Zeland., part II (1855) p. 294). *Compressum* cannot be used for the specific epithet on account of the earlier homonym *Stereocaulon compressum* Linds. (1866) (a *Sphaerophorus*-species).

St. foliolosum Nyl. var. *strictum* (Bab.) M. Lamb, *n. comb.* (Syn. *St. ramulosum* var. *strictum* Bab. in Journ. of Bot. IV (1852) p. 250; non *St. strictum* Th. Fr., De Stereoc. et Pilophor. Comment. (1857) p. 24).

St. lavicola H. Magn. apud Magnusson & Zahlbruckner in Ark. f. Bot. XXXI A, no. 6 (1944) p. 38, *emend.* M. Lamb. The type material contains two different species, one being *St. octomerellum* var. *sandwicense* (H. Magn.) M. Lamb, *n. comb.* (Syn. *St. sandwicense* H. Magn. in Ark. f. Bot. XXXI A, no. 6 (1944) p. 39). *St. lavicola* is therefore emended to include only the other species.

St. Meyeri Stein var. *farinosum* (Th. Fr.) M. Lamb, *n. comb.* (Syn. *St. ramulosum* δ. *farinosum* Th. Fr., De Stereoc. et Pilophor. Comment. (1857) p. 12).

St. octomerellum Müll. Arg. var. *sandwicense* (H. Magn.) M. Lamb, *n. comb.* (See under *St. lavicola*).

St. platycladum (M. Lamb) M. Lamb, *n. comb.* (Syn. *St. denudatum* var. *platycladum* M. Lamb in Nytt Mag. f. Naturvidensk. LXXX (1940) p. 278).

St. ramulosum (Sw.) Räusch. var. *assimile* (Nyl. emend. M. Lamb) M. Lamb, *n. comb.* (Syn. *St. assimile* Nyl. in Ann. Sci. Nat., Bot., sér. 4, XI (1859) p. 251 *pro parte*). Nylander's type material consists of a distinct variety of *St. ramulosum* mixed with *St. scutelligerum* Th. Fr.; the epithet *assimile* is therefore emended to apply only to the former, and transferred to varietal rank.

St. strictum Th. Fr. var. *lecanoreum* (Nyl.) M. Lamb, *n. comb.* (Syn. *St. lecanoreum* Nyl. in Flora, XLI (1858) p. 117, footnote).

St. vesuvianum Pers. This is conspecific with the well known *St. denudatum* Flk. (1819), and being an earlier epithet (1810) must replace the latter.

Subsp. *santorinense* (Steiner) M. Lamb, *n. comb.* (Syn. *St. denudatum* subsp. *santorinense* Steiner in Verhandl. Zool.-Bot. Ges. Wien, LXIX (1920) p. 90).

Var. *umbonatum* (Wallr.) M. Lamb, *n. comb.* (Syn. *Patellaria paschalis* γ. *umbonata* Wallr., Flora Cryptog. German. III (1831) p. 442).

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